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Shell structure of three littoral species of testate amoebae from the Black Sea (Rhizopodea: Protozoa)

Vassil Golemansky
Institut de Zoologie, Sofia, Bulgaria

and

Colin G. Ogden
Department of Zoology, British Museum (Natural History), London SW7 5BD, England

Introduction

Ultrastructural studies have been reported on both the shell and cytoplasm of testate amoebae from freshwater, moss and soil habitats. Since the first reports of Thomas (1958) and Thomas & Hovasse (1962) on the shell of the genus *Trinema,* several reports have dealt with these structures in other genera, for example *Euglypha* (Mercier *et al.,* 1964; Hedley & Ogden, 1973; Hedley *et al.,* 1974); *Arcella* (Camber *et al.,* 1963; Netzel, 1975; Moraczewski, 1971); *Centropyxis* (Netzel, 1976*a*; Hedley *et al.,* 1976); *Difflugia* (Netzel, 1976*b*; Ogden, 1979) and *Cryptodifflugia* (Hedley *et al.,* 1977). The diversity and complexity of the shell for most of the common freshwater species has been illustrated in the recent publication of an Atlas of Freshwater Testate Amoebae by Ogden & Hedley (1980).

The present work is a contribution to the ultrastructure of the shell of three species of testate amoebae which are found specifically amongst sand of the supralittoral region bordering marine waters.

Materials and Methods

Individual specimens were selected from samples collected from the shores of the Black Sea, Bulgaria during 1977. The animals were fixed in 3% glutaraldehyde in 0·1M cacodylic acid buffer and post-fixed in 1% osmium tetroxide, after fixation for about 10 minutes they were washed several times in distilled water. Each shell was manipulated using a single-hair brush onto small drops of Araldite arranged on an otherwise clean cover slip. The prepared cover slips were mounted onto standard Stereoscan stubs with Araldite, prior to coating evenly with a conducting layer of gold. The stubs were examined on a Stereoscan Mk II operating at 10kV and the results recorded on Ilford HP4 film.

Results

Pomoriella valkanovi Golemansky, 1970

This species is found in underground water littorals on sandy beaches of the Black Sea, where the salinity varies between 15–17·2‰. The shell is colourless or transparent. In outline it is pyriform with anterior region curved, and in transverse section it is circular (Figs 1 and 3). The aperture is circular or oval and bordered by organic cement (Fig. 4). The surface is covered with shell plates that abut against each other, without overlapping, and are joined by an abundance of organic cement (Fig. 2). The shell plates in the aboral region are long, oval, about 9–10µm in length and 6–7µm in width, and in the apertural region they are smaller, about 4–5µm long and 1–2µm in width. Unfortunately the specimens have bacteria and

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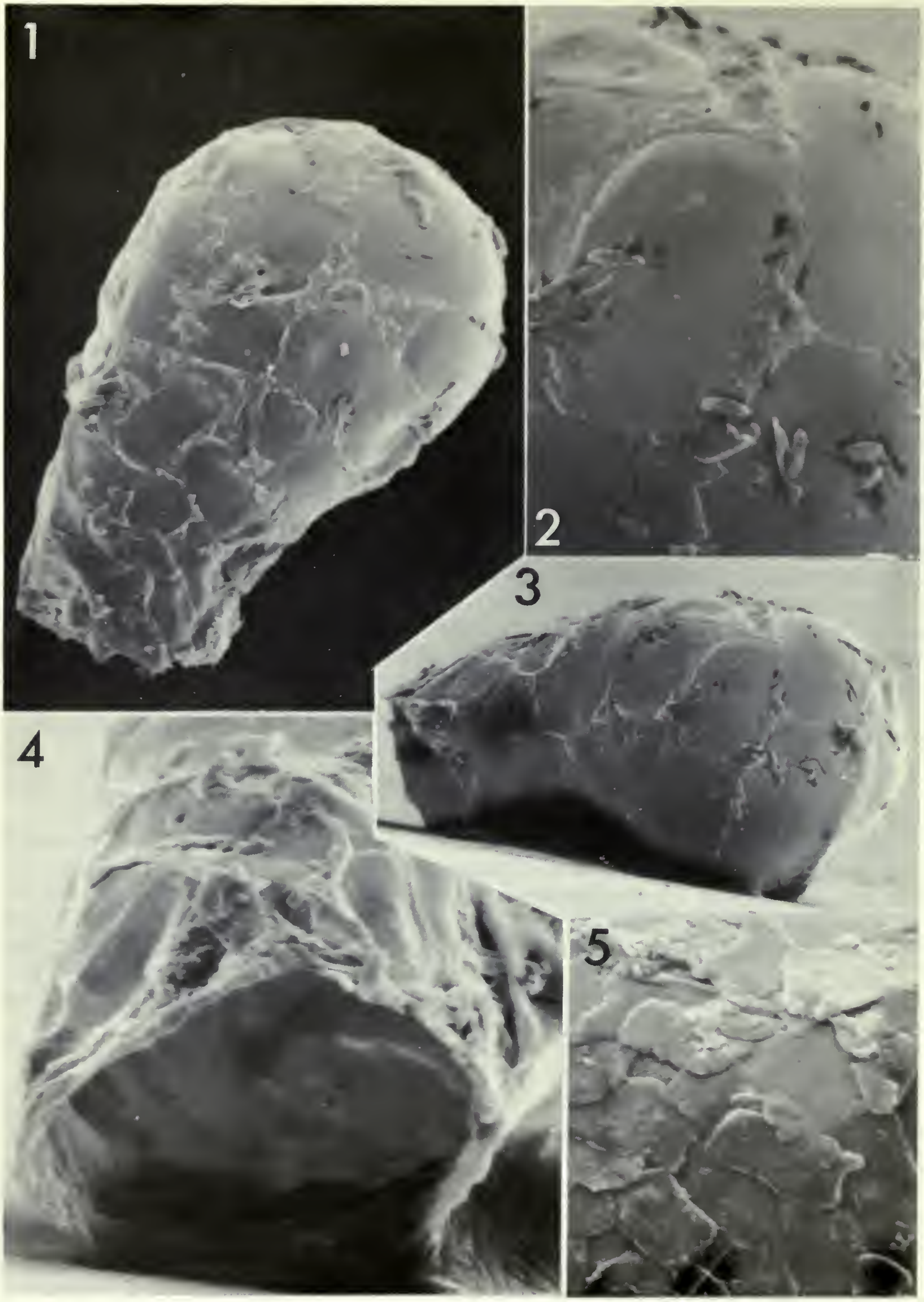
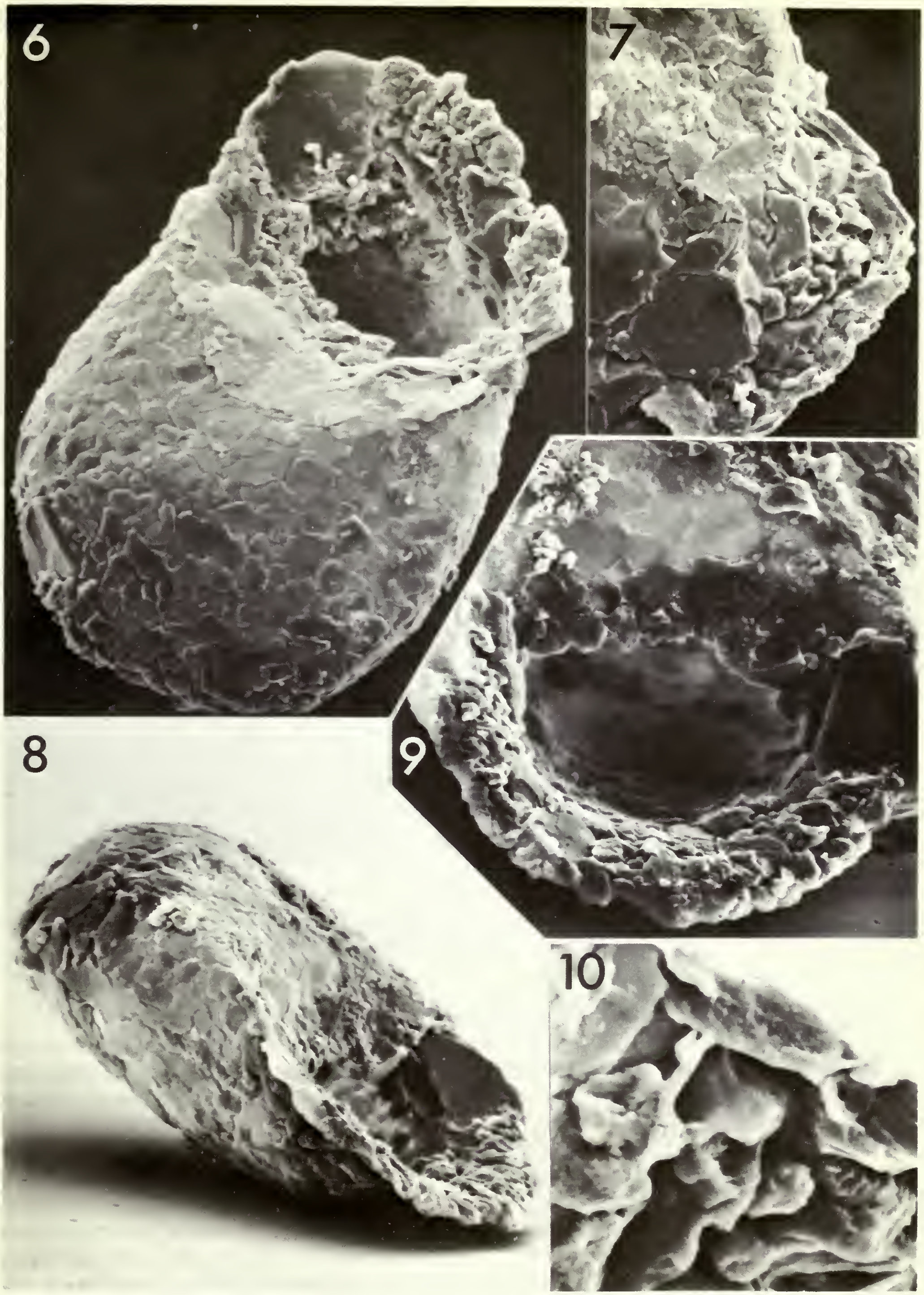


Figs 1–4 *Pomoriella valkanovi* Fig. 1. Lateral view × 2300 Fig. 2. Portion of shell surface, note the organic cement and adhering debris bordering the shell plates × 4800 Fig. 3. View to illustrate the slight curvature of the shell near the aperture × 1900 Fig. 4. Apertural view × 4900.

Fig. 5 Apertural surface of shell of *Centropyxiella arenaria*, to show the arrangement of flat particles × 3600.



Figs 6–10 *Centropyxiella arenaria* Fig. 6. Lateral view, note that most of the shell surface is smooth × 1350 Fig. 7. Aboral view of apertural disc-like extension to show the rough surface × 1400 Fig. 8. Latero-apertural view to illustrate the apertural extension × 1600 Fig. 9. Apertural view × 1950 Fig. 10. Detail of irregular particles forming the apertural extension × 4300.

debris adhering to portions of the shell surface, which obscured some detail. The two specimens examined measured 39; 45μm in length, 24; 21μm in diameter and the diameter of the aperture 13·5; 10·3μm respectively.

In the original description Golemansky (1970) described the shell plates as being rectangular, square or polygonal, sometimes rounded at the corners. It would seem, from the present observations, that the shell plates are usually rounded at the corners, but in all other respects agree with the earlier description.

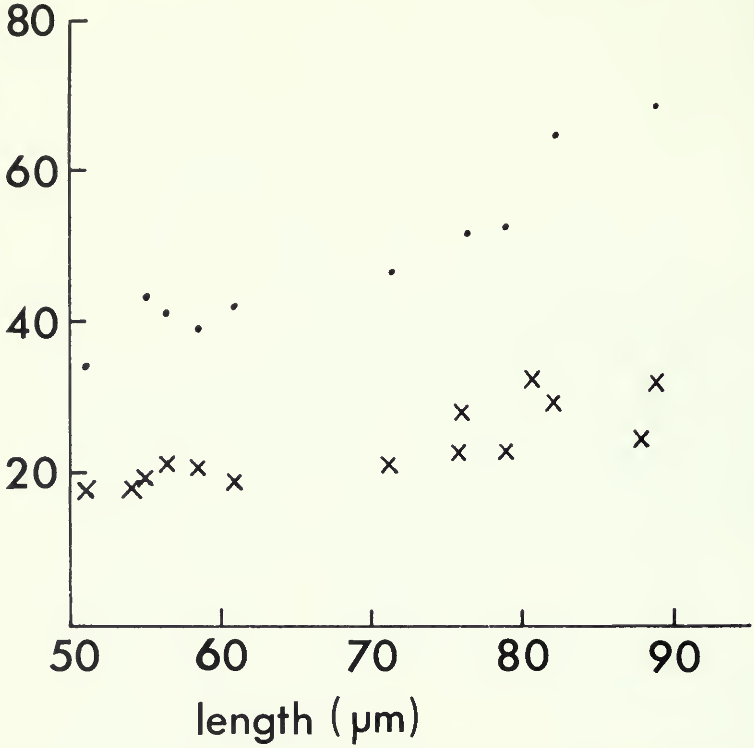


Fig. 11 Measurements of breadth (points) and diameter of aperture (crosses), for individual specimens of *Centropyxiella arenaria*, plotted against the shell length.

Centropyxiella arenaria Valkanov, 1970

This species appears to have a cosmopolitan distribution and is found in salinities varying from 26·1–37·8‰. The shell is colourless, ovoid in outline, sometimes having almost parallel lateral margins which curve evenly in the aboral region but often curve irregularly around the aperture (Fig. 6). In lateral view it is elliptical, tapering rapidly towards the aperture (Fig. 8). The aperture is oval and invaginated (Fig. 9). Most of the shell surface is smooth, and composed of overlapping, flattish particles of quartz held together by organic cement (Fig. 5). It would appear that the apertural surface is made of small flat particles, whilst the curved surface of the remainder of the shell is made from a mixture of small and large, flattish particles. The aperture is surrounded by a thickened, often rough, irregular disc-like extension composed of an assortment of quartz particles (Figs 6, 7 and 10).

In the original description Valkanov (1970) noted that the quartz particles bordering the aperture were larger than those of the shell, whilst Golemansky (1976) described some small specimens, 28–31μm long, with transparent organic shells and particles principally around the aperture. *Centropyxiella elegans* also described by Valkanov (1970) appears to differ in size alone, varying between 70–80μm in length, whereas *C. arenaria* reaches only 60μm.

Specimens of *C. arenaria* collected from the shore at Ostend, North Sea, varied between 35–60μm (Chardez, 1977), whilst those from the Guinea Coast, Atlantic Ocean, were 53–56μm in length (Golemansky, 1976). Measurements of specimens in this study suggest that the length varies between 54–89μm. Individual dimensions of the breadth and the diameter of the aperture are expressed graphically against shell length in Fig. 11. It is possible that both *C. arenaria* and *C. elegans* are present in our sample, but the number of specimens examined are insufficient to reach any conclusions and we have therefore referred to them collectively as *C. arenaria.*

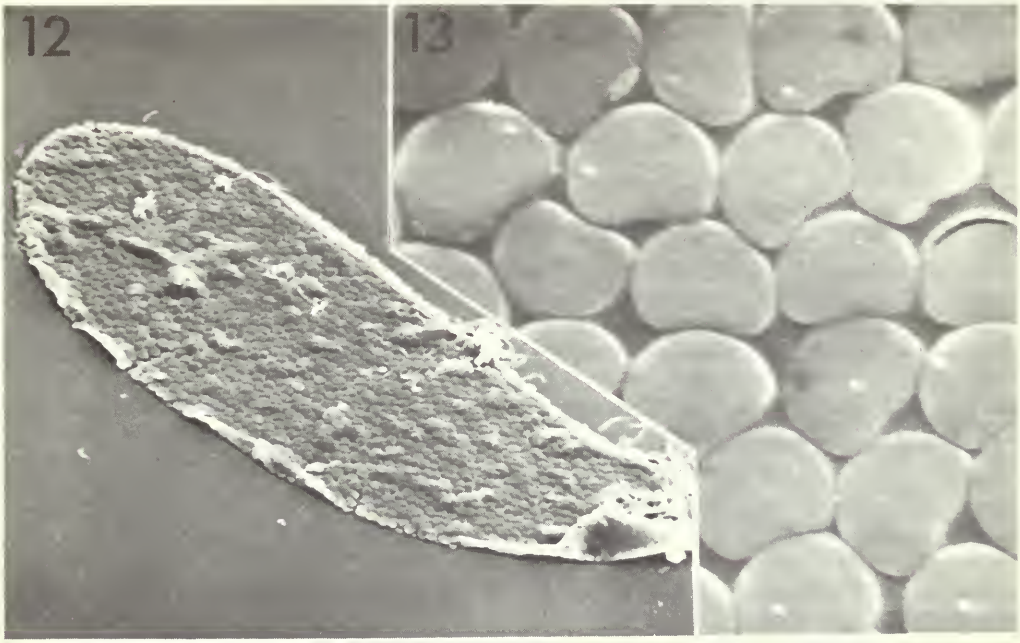


Fig. 12 Collapsed specimen of *Cyphoderia compressa* showing the arrangement of the shell plates × 820.

Fig. 13 Detail of kidney-shaped shell plates of *Cyphoderia compressa* × 9100.

Cyphoderia compressa Golemansky, 1979

This species was described recently from underground water littorals of marine beaches, and is similar to the common freshwater species *C. ampulla* (Ehrenberg, 1840). It is distinguished from *C. ampulla* by the strong lateral compression of the shell. In transverse section *C. compressa* is oval and appears to taper evenly along most of the shell length, whereas in *C. ampulla* the transverse section is circular and has the greatest diameter around the mid-point of the shell and tapers rapidly at both extremities. Unfortunately, as the shells of this species are fragile, they collapsed when air dried in preparation for scanning (Fig. 12).

In species of *Cyphoderia* there appears to be two main arrangements of the siliceous shell plates, these are (i) individually separate plates that lie close together and (ii) those that overlap. These arrangements have been described in detail by Penard (1902), Cash *et al.*, (1915) and more recently by Ogden & Hedley (1980). The shell plates of *C. compressa* (Fig. 13) are similar to those of *C. ampulla,* although the number of kidney-shaped plates – about 1·8μm long and 1·4μm wide – and the amount of visible organic matrix appears to be greater in the former species.

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Notes on the hydroid, *Synthecium evansi*

P. F. S. Cornelius

Zoology Department, British Museum (Natural History), London SW7 5BD, England

Synopsis

The Mediterranean hydroid, *Synthecium evansi* (Ellis & Solander, 1786), has been recorded twice from British waters but neither record can be proved. As the species has not been reported from Britain in the past 150 years it is now removed from the British list.

British records

Synthecium evansi (Ellis & Solander, 1786) is a large and distinctive hydroid recorded widely in the Mediterranean Sea. However, its first description was based on material said to have been 'brought from' Great Yarmouth, Norfolk, England. But the species has not been recorded from British waters for 150 years and the Norfolk record is in doubt. It is true that the collector, John Evans, worked for the East India Company and was based at Great Yarmouth. Further, George Johnston (1838) recorded that Evans sent specimens to James Petiver's once famous Museum in London and there seems no reason to doubt that he could have supplied the *S. evansi* material to Ellis. Indeed, Ellis often received specimens from traders and based several new species on them. For example Mediterranean material is mentioned in Ellis & Solander's book in five places (pp. 15, 27, 88, 101, 149) and other specimens, from still farther afield, were brought back by East India Company ships (p. 58, twice on p. 107). But as Ellis & Solander's book was posthumous to them both it is possible that the locality data did not receive Ellis' usual careful attention. Further, the illustrations of *S. evansi* were left out of the book and are to be published only now (Wells & Cornelius, in prep.). There was clearly some confusion about the first description and the Norfolk locality cannot be accepted without further proof.

Unfortunately some authors (Lamouroux, 1816; Johnston, 1838, 1847; Landsborough, 1852) repeated the Norfolk record and although it was overlooked by Hincks (1868) and later compilers its accuracy has not been questioned.

The only other British record is also suspect. Lamouroux (in Lamouroux, Bory de Saint-Vincent & Deslongchamps, 1824) stated that he had received material from 'the coast of England'. But this material was not mentioned in his two earlier books (Lamouroux, 1816, 1821); and no specimens were found in Lamouroux' collections by Billard (1909) and Redier (1967). Once again there is no proof that any specimens were collected in British waters.

Conclusion

There have been no records of *S. evansi* from Britain or anywhere else in NW Europe for 150 years. There is only a slim chance that such a large species would have been missed by the many collectors of this period and it seems right to take *S. evansi* off the British list.

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The life history and ecology of the aberrant bathypelagic genus *Benthomisophria* Sars, 1909 (Copepoda: Misophrioida)

G. A. Boxshall

Department of Zoology, British Museum (Natural History), South Kensington, London SW7 5BD, England

H. S. J. Roe

Institute of Oceanographic Sciences, Brook Road, Wormley, Godalming, Surrey

Introduction

The copepod order Misophrioida comprises the littoral genus *Misophria* Boeck, 1864 and the rare bathypelagic genus *Benthomisophria* Sars, 1909. The only published records of the latter genus are those of Sars (1909), Hulsemann & Grice (1964) and Tanaka (1966 – as *Misophria*). Little is known of the life history and ecology of either of the two *Benthomisophria* species, primarily because of the difficulty in obtaining large samples of these bathypelagic forms. In 1976 the Institute of Oceanographic Sciences commenced a total water column sampling programme, integrating midwater, near-bottom and benthic hauls. A new technique for taking near-bottom samples was employed and this is described in detail below. Analysis of the first complete series taken under this programme revealed large numbers of *Benthomisophria,* including many developmental stages. These specimens were found to belong to *B. palliata* Sars, 1909 and to *B. cornuta* Hulsemann & Grice, 1964. The 5 copepodid stages of *B. palliata,* 3 copepodid stages and male of *B. cornuta* are described for the first time. Notes on the vertical distribution of both species are presented, and phylogenetic relationships within the Misophrioida are examined.

Materials and methods

Sampling methods

The samples were taken with the acoustically controlled RMT 1+8 net system described in Baker, Clarke & Harris (1973). The small mouth area RMT 1 has a mesh size of 320 μm and the larger RMT 8 has a 4·5 mm mesh. The effective mouth areas of these nets vary with towing speed (Baker *et al.,* 1973; Roe & Baker, in prep.). The nets are opened and closed acoustically using a telemetering net monitor that activates a mechanical release gear. The monitor continuously telemeters the depth, temperature, speed and distance travelled (collectively called flow) and an indication of whether the nets are open or closed. This information is displayed on the ship on a modified Mufax facsimile recorder (Roe & Harris, in press).

The sampling programme required samples to be taken in discrete depth layers from just above the sea bottom to the surface. In order to fish the nets to within approximately 5m of the sea bed in depths of 4000m a system of bottom indicator switches was used. This consisted of 2 mercury switches, each encased in a streamlined protective housing, connected to the net monitor by a single protected conducting cable. The cable was fixed down the side wires of the nets to the weight bar, and the switches hung below this bar so that their estimated distances below the bottom bar when fishing were 5m and 20m respectively. The near-bottom hauls were made by paying out the net until it was within 20m of the bottom, as shown by the lower indicator switch hitting the sea bed and tilting so that the mercury within the switch made an electrical contact. This contact was telemetered back to the ship where it

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was displayed on the Mufax as a displacement of the net indicator trace. Paying out more warp caused the second switch to hit the sea bed, resulting in a further displacement of the net trace. The first shift in this trace therefore indicated that the net was about 20m above the sea bed and the second that it was about 5m above the bottom.

The net was then opened and maintained within this 5–20m layer by adjusting the amount of warp so that the 20m indicator was continuously registering with the 5m indicator appearing intermittently. Two hauls, Station numbers 9541 # 18 and 19 (Table 1), were made in this way. The remaining hauls sampled progressively further from the bottom.

Table 1 Station data of the hauls in which *Benthomisophria* spp. were found.

Station No.	Sounding range (m)	Mean Sounding (m)	Depth off bottom of sample (m)	Depth from surface of sample (m)	Duration of haul (H)
9541# 18	3974–4036	4005	5–20		6
#19	4008–4060	4031	5–20		6
#22	3856–3914	3883	20–100		6
#24	4000–4079	4035	100–500		6
#25	4008–4105	4058	500–1000		6
	Σ3856–4105	4002			
#26	3918–3945	3934		2510–3000	4
#27	3839–3889	3860		2000–2500	4
9131# 18	3870–3896	3884	20–100		4
#19	3957–4036	3998	100–500		5
#23	3865–3934	3905	500–1000		4

Since the net was a considerable distance behind the ship during these deep hauls the bottom depth over which it was actually fishing was derived as follows. The sounding beneath the ship was recorded on a Precision Echo Sounder (PES) continuously during the paying out and retrieval of the nets and periodically throughout the fishing periods. From these data a bathymetric chart of the area was subsequently constructed. The bottom was found to be essentially flat with the soundings in each haul varying by less than 100m (Table 1) in a total distance travelled over the ground of between 19·1–21·9 Km. The position of the net whilst fishing was calculated by triangulation – knowing at a given moment the ship's course, the depth below the ship and the amount of wire out. Because the gradient of the bottom was so slight it was possible to ignore errors in triangulating the net position caused by a changing depth and by lateral displacement of the net behind the ship. This calculated net track was then superimposed upon the bathymetric chart and the mean bottom depth over which the net had fished was derived from the soundings taken at every one minute of longitude on the chart.

Station number 9541 # 22 (Table 1) fished between about 20 and 100m off the bottom. The 20m indicator switch was used to determine the lower limit of the haul whereas the upper limit was obtained from the monitor depth. The net was fished so that depth according to the monitor was within 100m of the bottom sounding at the position derived from triangulating back along the ship's track. All subsequent hauls up to 1000m off the bottom were fished using the monitor in this way. Table 1 gives the sounding ranges and mean soundings for these hauls. The depths of samples taken at up to 1000m off the bottom are expressed in terms of distance off the bottom. The depths of hauls shallower than 1000m off the bottom were taken directly from the monitor, i.e. measured from the surface.

The absolute depths fished using the techniques described are probably inaccurate, as both PES and monitor depths are subject to error due to the changes in water density and temperature, but they are accurate relative to both the bottom and each other. Any effect which the bottom may have on the bathypelagic animal populations is presumably proportional to their distance away from it, and these relative distances are consequently much more important ecologically than a possible error of a few metres in absolute depth. The changeover depth to conventional surface measurements was arbitrary. It may be shown subsequently that a distance of 1000m off the bottom is not the optimum changeover point although Brewer, Spencer, Biscaye, Hanley, Sachs, Smith, Radar & Fredericks (1976) have found that this distance is approximately the top of the nepheloid layer, at least further north in the Atlantic.

Most of the samples used here (Table 1) were taken at Station 9541 in April 1977, within an area 20°0·6′N to 20°25·4′N and 21°9·6′W to 21°56·4′W. These are the hauls described above. Station 9131 was fished in the same area in November 1976 as a preliminary to the detailed programme of April 1977. The near-bottom samples from this station were taken in a similar way to that described above but only a single bottom indicator switch was used.

Material

The samples were preserved on the ship in 5% formalin. Subsequently they were transferred to a preserving fluid based on that of Steedman (1974) and the *Benthomisophria* spp. were picked out of the total RMT 1 and RMT 8 samples. A small triangular net (the DN) of mesh size 61µm was added to the RMT 1+8 combination net to sample small zooplankton. The DN catch was examined for one haul (9541 # 24) and contained 3 specimens of *B. palliata* and a single *B. cornuta*. All the material came from the hauls shown in Table 1 except for a single adult female *B. palliata* which was found in a RMT 8 sample fished between 3000 and 3500m in a position 44°27′N 12°44′W. The numbers of *B. palliata* and *B. cornuta* caught are given in Tables 2 and 3. No specimens of either species were found in hauls shallower than 2000m.

Undamaged specimens were measured from the tip of the cephalothorax to the end of the caudal rami. The numbers measured are also given in Tables 2 and 3. There was no difference in the size distribution of either species between stations 9131 and 9541 and data from both stations have been combined in the frequency distributions of body length (Figs 14 & 15).

Table 2 The numbers of each stage of *Benthomisophria palliata* found and measured.

Net	RMT 1							RMT 8			
Stage	I	II	III	IV	V	♀	♂	IV	V	♀	♂
Station											
9541#18		38	13	41	14	16	11		1	5	4
19		7	10	63	17	39	38		1	25	17
22		5	9	12	13	22	4	2	5	7	1
24	7	44	17	15	15	13	17		5	4	2
25			3	8	26	3	6		1		1
26	1	5	6	11	6	5	2			4	
27						1					
9131#18		8	16	26	10	8	4		2	13	2
19	5	37	33	22	12	17	4	1	4	9	1
23	not examined									9	3
8509#20										1	
Total of RMT1, RMT8 + DN	14	144	107	201	132	203	117				
No. measured	14	133	98	151	103	186	93				

Table 3 The numbers of each stage of *Benthomisophria cornuta* found and measured.

Net	RMT 1				
Stage Station	III	IV	V	♀	♂
9541#18	1		2	2	2
19				1	1
22	1		1	1	
24		2		1	1
25			1	1	
26			3	3	
9131#18		4	4	1	
19	1	3			2
Total inc. DN	4	9	11	10	6
No. measured	4	9	11	10	6

The copepods were stained in chlorazol black in lactophenol, dissected and examined in lactophenol and mounted as permanent preparations in polyvinyl lactophenol. They were examined by phase contrast microscopy and drawings were made with the aid of a camera lucida.

Descriptions

Family **MISOPHRIIDAE**

Genus ***BENTHOMISOPHRIA***

Benthomisophria palliata SARS, 1909

Benthomisophria palliata G. O. Sars, 1909: 1–4, Fig. 1.
Misophria japonica O. Tanaka, 1966: 51–55, Figs 1–2.

The descriptions of the adults of both sexes and of the copepodid stages of *B. palliata* are based on the examination of a total of 918 specimens. The specimens were sorted, on morphological criteria, into copepodid stages I to V, adult male and adult female.

COPEPODID I

Prosome (Fig. 1A) large, 5-segmented and comprising 86% of total body length; rounded anteriorly, with greatest width at posterior border of cephalosome. Last prosome somite with parallel sides and small postero-lateral projections. Urosome 1-segmented, sub-rectangular. Caudal rami apparently bearing only 1 dorsal and 2 distal armature elements.

First antenna (Fig. 1B) 6-segmented; with incomplete armature, elements present as follows: I – 2+1 spine, II – 1 aesthete, III – 0, IV – 0, V – 1, VI – 6. Second antenna (Fig. 1C) biramous with 5-segmented exopod and 3-segmented endopod, first segment of which is partially fused to basis. Labrum large, fused to rostrum. Mandible (Fig. 1D) blade with 4 large teeth and several other elements; mandibular palp biramous, with 2-segmented endopod and 4-segmented exopod. First maxilla (Fig. 1E) gnathobase with 2 naked and 10 spinulate setae; rudimentary outer lobe on basal segment bearing at least 3 setae; inner lobes 1 and 2 about equal in size and armed with 4 and 3 setae respectively; distal endopod segment with at least 3 distal setae (some elements missing), proximal segment also with 3 distal setae; exopod 1-segmented, armature incomplete. Second maxilla (Fig. 1F) apparently 5-segmented: first segment with 2 inner lobes both armed with 3 setae; second segment with

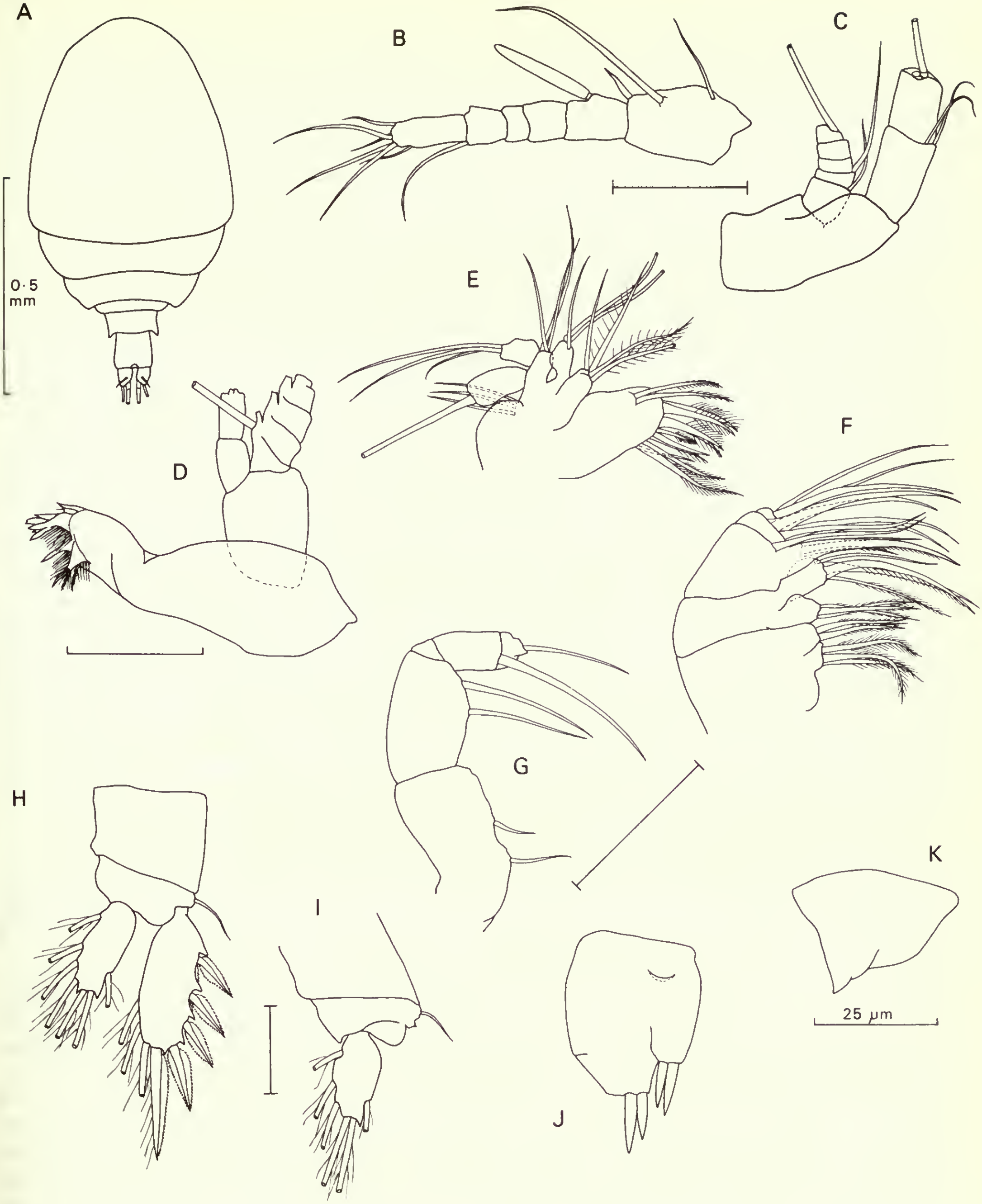


Fig. 1 *B. palliata* Copepodid I. A, dorsal; B, first antenna; C, second antenna; D, mandible; E, first maxilla; F, second maxilla; G, maxilliped; H, Leg 1; I, leg 2; J, leg 3; K, leg 4. Scales 100µm unless otherwise indicated.

2 inner lobes bearing 3 and 4 setae; third segment extended medially into a large curved process carrying 2 setae basally; two distal segments bearing a total of 10 setae. Maxilliped (Fig. 1G) 5-segmented, armature incomplete in all available specimens.

Thoracic legs 1 to 4 present; legs 1 and 2 biramous, leg 3 bilobed and leg 4 rudimentary. Leg 1 (Fig. 1H) with 2-segmented sympod and 1-segmented rami; exopod bearing 4 outer margin spines, an apical spine and 3 inner margin setae; endopod with 1 outer, 2 distal and 4 inner margin setae. Leg 2 (Fig. 1I) segmentation as for leg 1; exopod missing in all specimens; endopod with 1 outer, 2 distal and 3 inner margin setae. Leg 3 (Fig. 1J) a broad flattened structure, bilobed distally with each lobe bearing 2 apical armature elements. Leg 4 (Fig. 1K) rudimentary, comprising a spinous process on a broad base.

Body length ranging from 0·69 to 0·95mm, with a mean of 0·79mm (based on 14 specimens).

COPEPODID II

Prosome (Fig. 2A) large, 4-segmented; first pedigerous somite incorporated into cephalosome, but with some indication of surture line marking the boundary. Urosome (Fig. 2B) 2-segmented; first segment with small processes at postero-lateral angles, second segment sub-rectangular. Caudal rami with 1 dorsal, 1 lateral and 2 distal elements.

First antenna (Fig. 2C) 9-segmented; armature incomplete, elements present as follows: I – 4, II – 0, III – 1 spine, IV – 1 aesthete, V – 1, VI – 1, VII – 0, VIII – 2, IX – 6 + 1 aesthete. Second antenna as in copepodid stage I but with exopod apparently comprising 5 distinct segments (Fig. 2D) and possibly a sixth segment fused to the basis; each of first 4 distinct segments bearing 1 seta, terminal segment with at least 1 element. Labrum, mandibles, maxillae and maxilliped as in adult.

Leg 1 (Fig. 2E) biramous, with 2-segmented rami; exopod segment 1 with 1 outer spine, inner seta missing; exopod segment 2 missing; endopod segment 1 with 1 inner seta, segment 2 with 1 outer, 2 distal and 4 inner margin setae. Leg 2 (Fig. 2F) as for leg 1 except endopod segment 2 with only 3 inner margin setae. Leg 3 (Fig. 2G) with 2-segmented sympod, biramous but with both rami missing in all specimens. Leg 4 (Fig. 2H) a flattened structure, bilobed distally with each lobe carrying 2 apical armature elements.

Body length ranging from 0·76 to 1·33mm, with a mean of 1·03mm (based on 133 specimens).

COPEPODID III

Prosome (Fig. 2I) large, 4-segmented, with first pedigerous somite fully incorporated into cephalosome. Urosome (Fig. 2J) 3-segmented; first segment with leg 5 present, second segment with rudiment of leg 6 present, third segment sub-rectangular. Caudal rami with 6 armature elements.

First antenna (Fig. 2K) 12-segmented; armature incomplete, elements present as follows: I – 1, II – 7, III – 2, IV – 0, V – 1, VI – 1 spine, VII – 1 + 1 aesthete, VIII – 1, IX – 1, X – 0, XI – 1, XII – 6 + 1 aesthete. Second antenna, labrum, mandible, maxillae and maxilliped as in adult.

Leg 1 (Fig. 3A) biramous, with 2-segmented rami; exopod segment 1 with 1 outer spine and 1 inner seta, segment 2 with 3 outer spines, 1 apical spine and 4 inner margin setae; endopod segment 1 with 1 inner seta, segment 2 with 1 outer, 2 distal and 5 inner margin setae. Leg 2 (Fig. 3B) as for leg 1 except exopod segment 2 missing in all specimens, and endopod segment 2 with only 4 inner margin setae. Leg 3 (Fig. 3C) with both rami 2-segmented but incomplete in material available. Leg 4 (Fig. 3D) with 2-segmented sympod, biramous but with both rami missing in all specimens.

Leg 5 (Fig. 2L) 1-segmented, with 1 inner proximal and 3 distal setae. Leg 6 (Fig. 2M) represented by an unarmed spinous process.

Body length ranging from 0·99 to 1·71mm, with a mean of 1·29mm (based on 98 specimens).

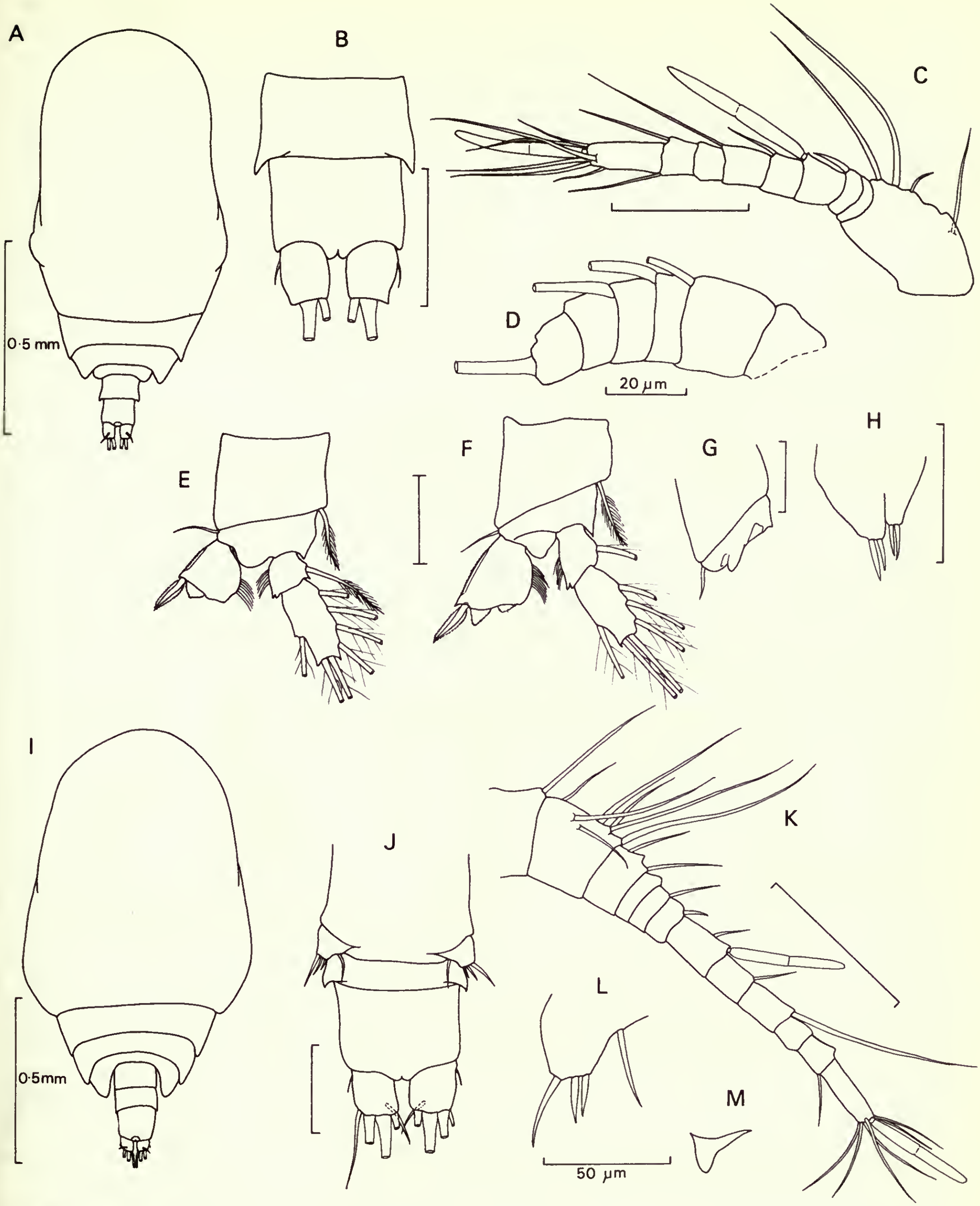

A
B
C
D
E
F
G
H
I
J
K
L
M
0·5 mm
20 µm
0·5mm
50 µm

Fig. 2 *B. palliata* Copepodid II & III. A, Copepodid II, dorsal; B, urosome, ventral; C, first antenna; D, exopod of second antenna; E, leg 1; F, leg 2; G, leg 3; H, leg 4; I, Copepodid III, dorsal; J, urosome, ventral; K, first antenna; L, leg 5; M, leg 6. Scales 100µm unless otherwise indicated.

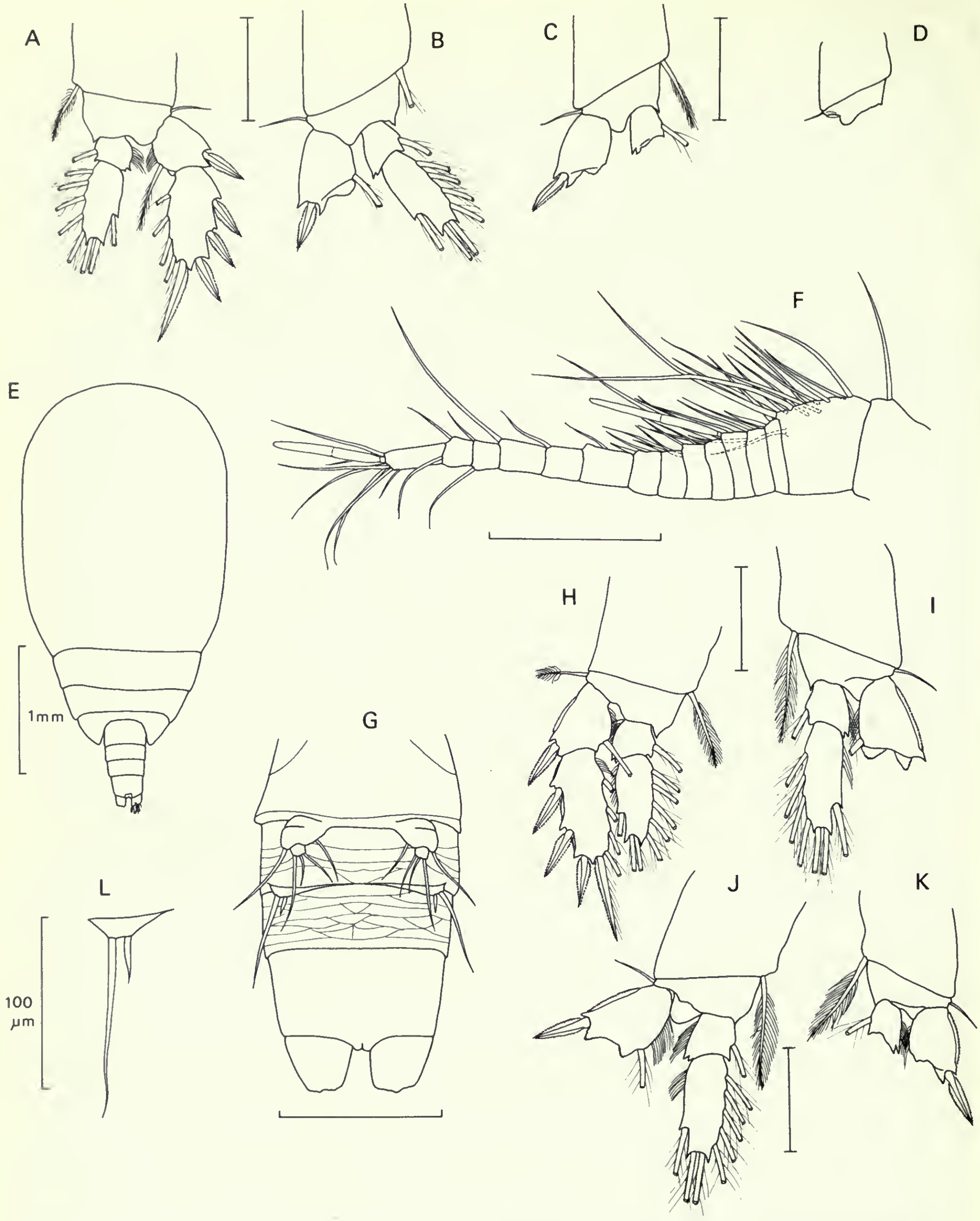


Fig. 3 *B. palliata* Copepodid III & IV. A, Copepodid III leg 1; B, leg 2; C, leg 3; D, leg 4; E, Copepodid IV, dorsal; F, first antenna; G, urosome, ventral; H, leg 1; I, leg 3; J, leg 2; K, leg 4; L, leg 6. Scales 200µm unless otherwise indicated.

COPEPODID IV

Prosome (Fig. 3E) large, 4-segmented. Urosome (Fig. 3G) 4-segmented; first and second segments bearing legs 5 and 6 respectively; segments 1 to 3 all with conspicuous reticulate surface markings; urosome segment 4 without surface markings.

First antenna (Fig. 3F) 15-segmented; armature elements present as follows; I – 1, II – 12, III – 2, IV – 3, V – 2 + 1 aesthete, VI – 2, VII – 3 + 1 aesthete (missing from figured specimen), VIII – 2, IX – 1 + 1 spine, X – 1, XI – 1, XII – 1, XIII – 2, XIV – 2, XV – 7 + 1 aesthete. Second antenna, labrum, mandible, maxillae and maxilliped as in adult.

Leg 1 (Fig. 3H) and leg 2 (Fig. 3J) as in Copepodid III stage, except endopod segment 2 of leg 2 now with 5 inner margin setae. Leg 3 (Fig. 3I) exopod segment 1 with 1 outer spine and 1 inner seta, segment 2 missing in all specimens; endopod segment 1 with 1 inner seta, segment 2 with 1 outer, 2 distal and 4 inner margin setae. Leg 4 (Fig. 3K) biramous, both rami 2-segmented, armature and rami incomplete in all available specimens.

Leg 5 (Fig. 3G) 2-segmented; basal segment with indication of subdivision laterally and armed with 1 inner and 1 outer seta; second segment with 3 apical setae. Leg 6 (Fig. 3L) a small process with 1 long and 1 short apical seta.

Body length ranging from 1·41 to 2·55mm, with a mean of 1·88mm (based on 151 specimens).

COPEPODID V

Prosome (Fig. 4A) large, 4-segmented, with epimeral plates of last free thoracic somite not acutely pointed. Urosome 5-segmented; segments 1 to 4 with reticulate surface markings, segment 5 without surface markings. Caudal rami (Fig. 4B) with 6 armature elements.

First antenna (Fig. 4C) 17-segmented, armature elements present as follows: I – 1, II – 10, III – 2, IV – 8, V – 1 + 1 aesthete, VI – 2, VII – 1 + 1 aesthete, VIII – 2, IX – 2, X – 2, XI – 2, XII – 2, XIII – 1, XIV – 0, XV – 2, XVI – 2 + 1 aesthete, XVII – 7 + 1 aesthete. Second antenna, labrum, mandible, maxillae and maxilliped as in adult.

Legs 1 to 4 (Figs 4D–G) biramous, with 3-segmented rami; armature formula as follows:

	coxa	basis	endopod	exopod
leg 1	0 – 1	1 – 0	0 – 1 ; 0 – 2 ; 1,2,3	I – 1 ; I – 1 ; missing
leg 2	0 – 1	1 – 0	0 – 1 ; 0 – 2 ; 1,2,3	I – 1 ; I – 1 ; III,I,5
leg 3	0 – 1	1 – 0	0 – 1 ; 0 – 2 ; missing	I – 1*; I – 1; missing
leg 4	0 – 1	1 – 0	0 – 1 ; 0 – 2* ; missing	I – 1 ; I – 1 ; missing

*elements missing but presumed present.

Leg 5 (Fig. 4H) as in adult. Leg 6 (Fig. 4I) a process armed with an outer plumose seta and 2 unequal apical elements.

Body length ranging from 2·01 to 3·75mm, with a mean of 2·71mm (based on 103 specimens).

ADULT MALE

Prosome (Fig. 5A) comprising 70 to 75% of total body length; epimeral plates of last free thoracic somite produced posteriorly and provided with expanded hyaline areas laterally. Urosome 6-segmented; segments 1 to 5 with reticulate surface markings (not figured), segment 6 with surface denticulations.

First antenna (Fig. 4J) apparently 16-segmented and geniculate, with the articulation between segments XIV and XV; aesthetes present on segments I, II (2), III, V, VII, X, XI, XIII, XV and XVI (2); segment XV also with a long spiniform process originating near base of aesthete; other armature elements present but omitted from figure.

All other appendages as for adult female except leg 6. Leg 6 (Fig. 5E) a process with a plumose outer seta, a long plumose apical seta and a short inner spiniform element.

Body length of males ranging from 2·70 to 4·72mm, with a mean of 3·75mm (based on 93 specimens).

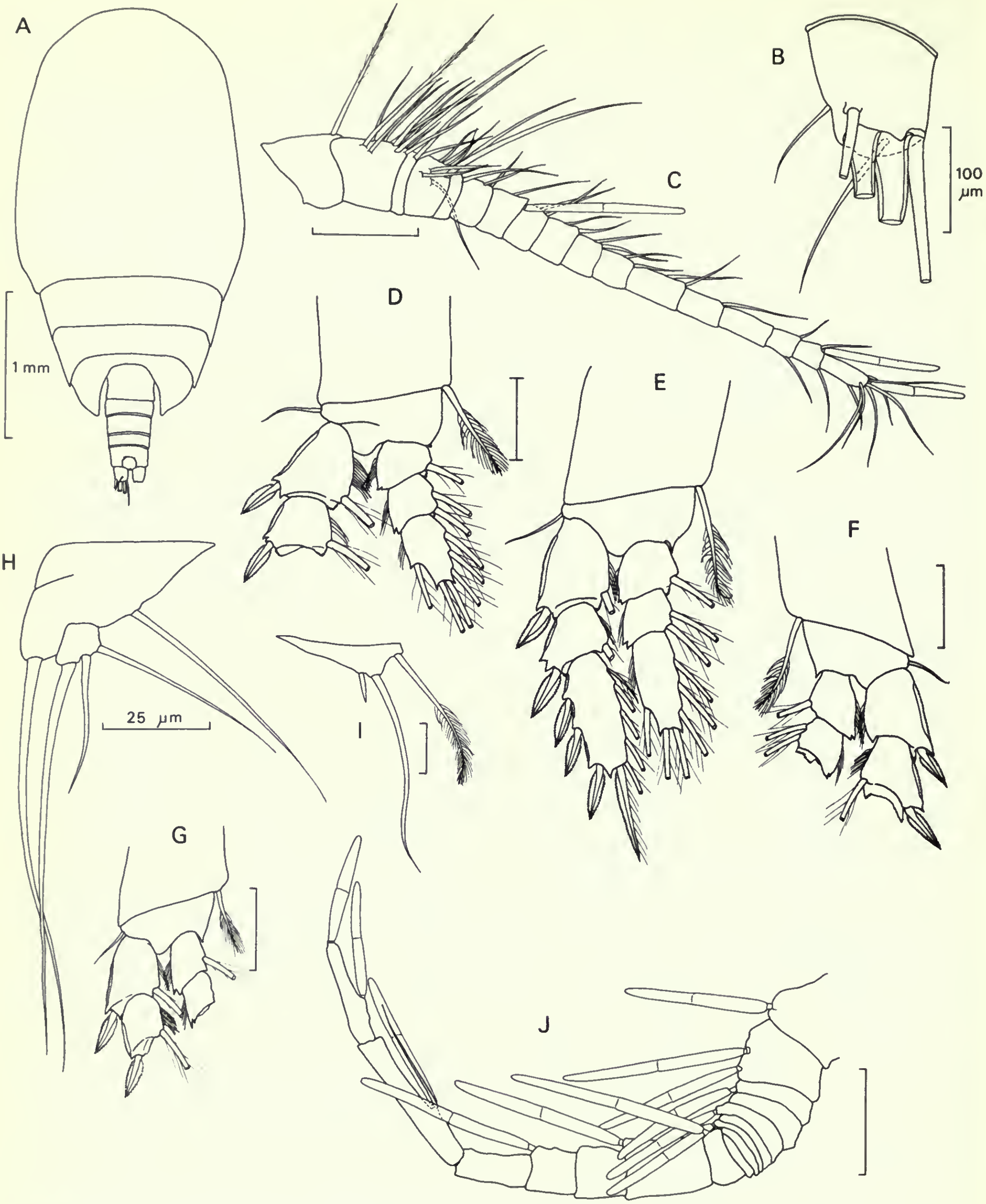


Fig. 4 *B. palliata* Copepodid V & adult male. A, Copepodid V, dorsal; B, caudal ramus, ventral; C, first antenna; D, leg 1; E, leg 2; F, leg 3; G, leg 4; H, leg 5; I, leg 6; J, Adult male first antenna (with setae omitted). Scales 200µm unless otherwise indicated.

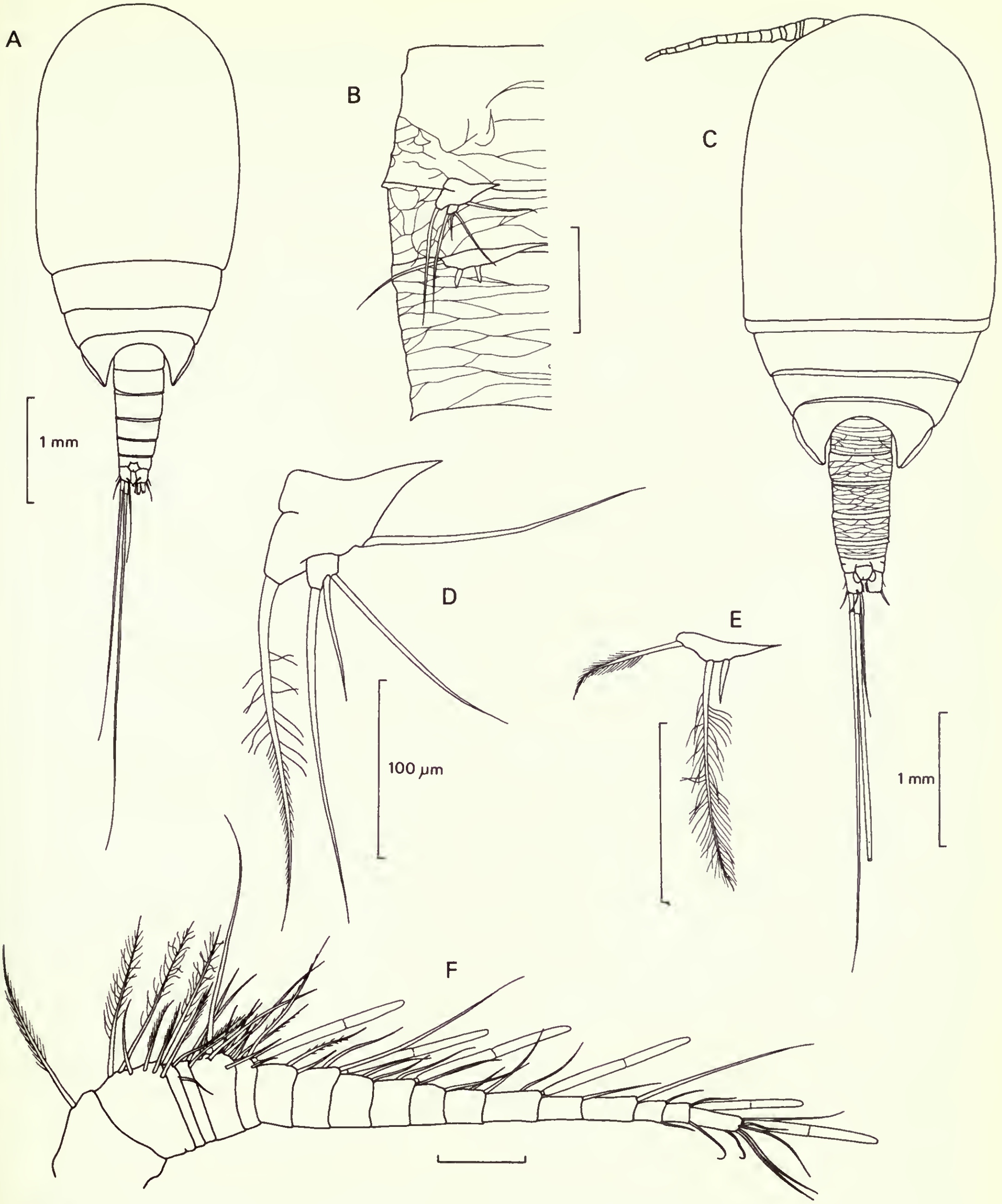


Fig. 5 *B. palliata* Adult male & female. A, Male, dorsal; B, Female urosome, ventral; C, Female, dorsal; D, leg 5; E, Male leg 6; F, Female first antenna. Scales 200μm unless otherwise indicated.

ADULT FEMALE

Prosome (Fig. 5C) large, 4-segmented with reticulate surface markings (not shown in Fig. 5C); segments 1 to 3 with strips of hyaline membrane dorsally along their posterior borders; segment 4 with posteriorly produced epimeral plates and with expanded hyaline areas laterally. Urosome (Fig. 5B) 6-segmented; segments 1 to 5 with reticulate surface markings, segment 6 with surface denticulations.

Labrum (Fig. 7B) strongly developed, fused to rostrum and projecting postero-ventrally from ventral body surface.

First antenna (Fig. 5F) 18-segmented; armature elements as follows: I – 1, II – 7, III – 2, IV – 2, V – 10, VI – 2 + 1 aesthete, VII – 2, VIII – 2 + 1 aesthete, IX – 2, X – 2 + 1 aesthete, XI – 1, XII – 2, XIII – 1 + 1 aesthete, XIV – 1, XV – 1, XVI – 2, XVII – 2 + 1 aesthete, XVIII – 6 + 1 aesthete.

Second antenna (Fig. 6A), basis with 1 outer distal seta; endopod 3-segmented, exopod with 5 distinct segments and possibly a sixth fused to basis. Endopod segment 1 with 1 outer margin seta, segment 2 with 3 outer margin setae and segment 3 with 6 long plumose apical setae. Exopod with 1 unilaterally pinnate seta on each of the first 4 distinct segments, and with 3 similar setae on terminal segment.

Mandible (Fig. 6B) blade with 8 main elements on distal margin (numbered 1–7 on Fig. 6B as element 8 is identical to element 7). Mandibular palp biramous, with 2-segmented endopod and 4-segmented exopod; endopod segments 1 and 2 bearing 1 and 2 setae respectively; exopod segments 1 to 4 bearing 1,1,1 and 3 long plumose setae respectively.

First maxilla (Fig. 6C) gnathobase with 15 elements; inner lobes 1 and 2 with 6 and 4 plumose setae respectively; outer lobe rudimentary, represented by 7 plumose setae on surface of segment; endopod apparently 2-segmented with distal segment positioned at an angle of 90° to proximal segment; proximal segment with 4 plumose setae apically, distal segment with 4 naked setae medially, 1 naked and 4 plumose setae apically; exopod 1-segmented, with 2 plumose setae medially and 5 long plumose setae distally.

Second maxilla (Fig. 6D–E) apparently 6-segmented; first segment with 5 plumose setae on proximal inner lobe and 3 on distal inner lobe; second segment with 2 inner lobes, each bearing 3 apical setae; third segment produced medially into a curved claw armed with 2 slender naked setae near its base; segments 4 to 6 bearing a total of 11 elements, 7 strong curved setae armed with 1 or 2 rows of pinnules and 4 slender naked setae.

Maxilliped (Fig. 6F) apparently 5-segmented; first segment with a single pinnate seta on a raised denticulated area situated proximally on the medial surface, a group of 1 small naked seta and 2 pinnate setae on another raised denticulated area in the middle, and 2 pinnate setae distally; second segment with a medial row of pinnules, 3 pinnate setae distally on medial margin and 3 areas of denticulations; third segment small and armed with a single pinnate seta; fourth segment partially subdivided into 3 portions each bearing 1 seta; fifth segment very small, bearing 4 slender setae.

Legs 1 to 4 (Figs 7C–F) biramous, with 3-segmented rami; armature formula as follows:

	coxa	basis	endopod	exopod
leg 1	0 – 1	1 – 0	0 – 1 ; 0 – 2 ; 1,2,3	I – 1 ; I – 1 ; III,I,4
leg 2	0 – 1	1 – 0	0 – 1 ; 0 – 2 ; 1,2,3	I – 1 ; I – 1 ; III,I,5
leg 3	0 – 1	1 – 0	0 – 1 ; 0 – 2 ; 1,2,3	I – 1 ; I – 1 ; III,I,5
leg 4	0 – 1	1 – 0	0 – 1 ; 0 – 2 ; missing	I – 1 ; missing

Pinnule rows present on lateral margins of all endopod segments and medial margins of all exopod segments. Lateral margins of all exopod segments armed with strips of serrated membrane. All outer margin spines bilaterally serrate, apical spines on exopods of legs 2 and 3 bilateraly serrate, that on leg 1 unilaterally serrate.

Leg 5 (Fig. 5D) 2-segmented; proximal segment with indication of suture line laterally, bearing a long outer seta apically and a medium length seta on inner margin; distal segment

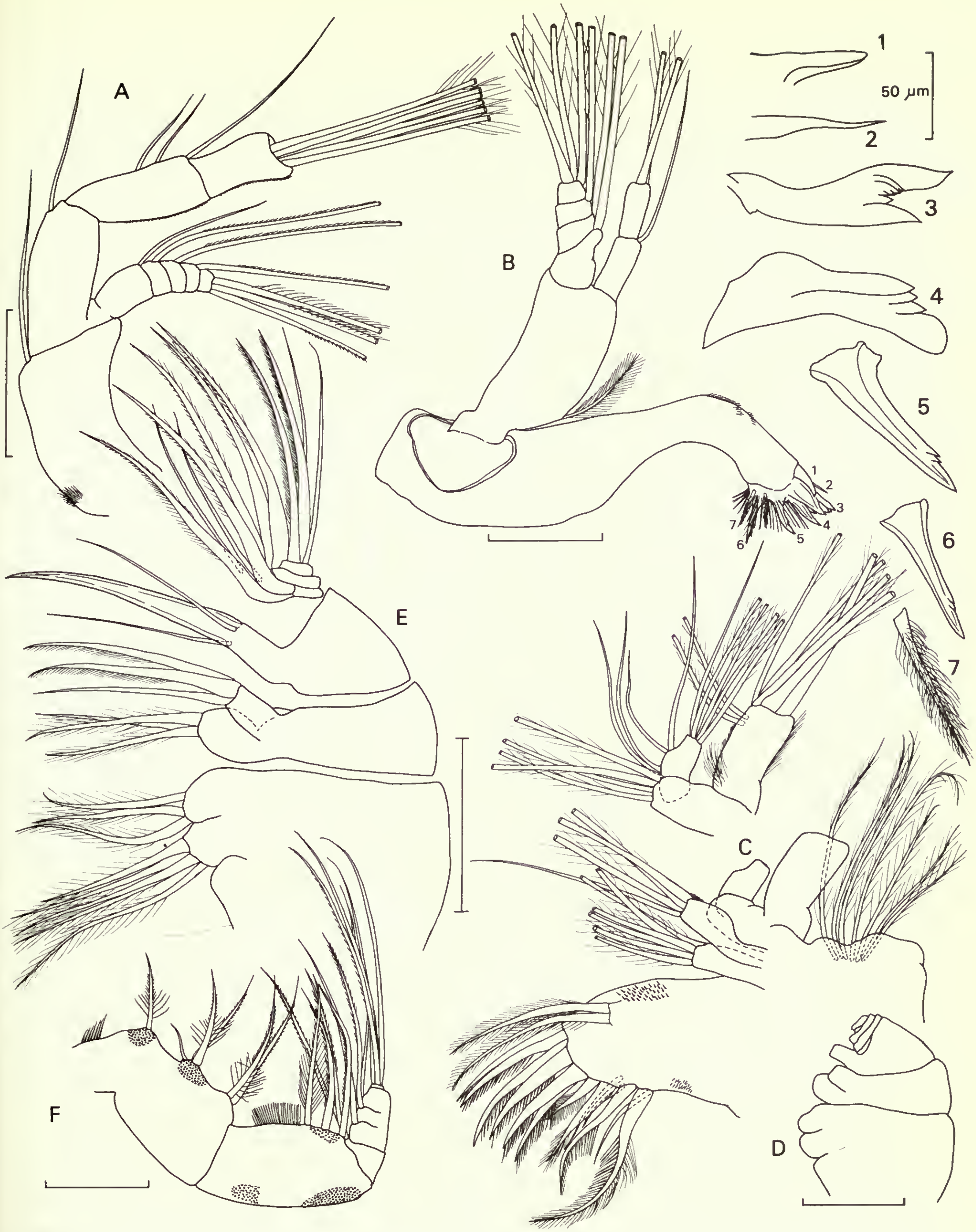


Fig. 6 *B. palliata* Adult female. A, second antenna; B, mandible – showing armature elements 1–7 enlarged; C, first maxilla – with rami separated from limb; D, second maxilla – showing segmentation; E, second maxilla with segments separated from each other; F, maxilliped. Scales 200μm unless otherwise indicated.

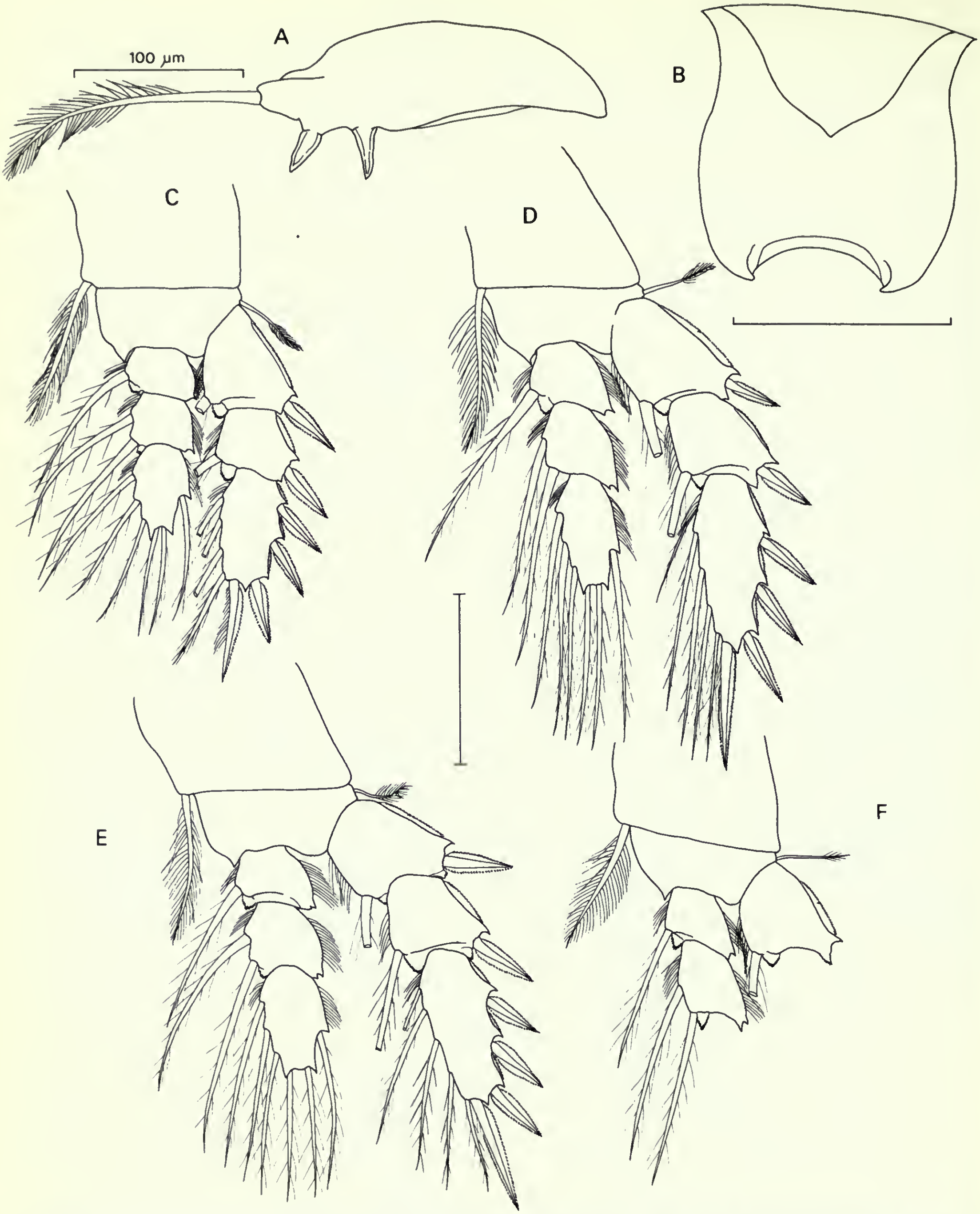


Fig. 7 *B. palliata* Adult female. A, leg 6; B, labrum, ventral; C, leg 1; D, leg 2; E, leg 3; F, leg 4. Scales 0·5mm unless otherwise indicated.

bearing 3 unequal setae along oblique distal margin. Leg 6 (Fig. 7A) a broad plate produced into a small process laterally, bearing a long plumose seta on its apex, and with 2 short spiniform elements on lateral portion of posterior margin.

Body length of females ranging from 2·88 to 5·70mm, with a mean of 4·0mm (based on 186 specimens).

MATERIAL EXAMINED

1♀, 1♂ and 1Co.V; S.A.S. *Le Prince Albert de Monaco,* Stn 2738 Côte W. du Portugal, 1908; donated by G. O. Sars, stored in the Musée Océanographique de Monaco.

203♀♀, 117♂♂, 132 Co.V, 201 Co.IV, 107 Co.III, 144 Co.II, 14 Co.I; 'Discovery' Stns 9541, 9131 and 8509 (see Table 2); BM(NH) registration numbers 1979.1–10 (♀♀), 1979.11–20 (♂♂), 1979.21–30 (Co.V), 1979.31–40 (Co.IV), 1979.41–50 (Co.III), 1979.51–60 (Co.II) and 1979.61–70 (Co.I).

REMARKS

A certain amount of confusion has been caused by inconsistencies in the original description of *B. palliata* (Sars, 1909). The type 'specimen' figured by Sars exhibits features characteristic of two different life cycle stages, i.e. the 6-segmented urosome of an adult female and the 17-segmented first antenna of a Copepodid V stage. It is probable that Sars added the first antennae to his drawing of the body of an adult female. In an attempt to resolve this situation Sars' material of *B. palliata,* stored in the Musée Océanographique de Monaco, was examined. This material comprises an adult female (with a 6-segmented urosome and 18-segmented first antenna), an adult male and a Copepodid V stage (with a 5-segmented urosome and 17-segmented first antenna). If this is the type material it would provide confirmation that Sars' figured 'specimen' combines features of both adult female and Copepodid V. However, it is not certain that this is the type material because the label with the material gives only one station (No. 2738) whereas Sars (1909) states that his 3 type specimens were taken at 3 separate stations (Nos. 819, 1479 and 2108).

Misophria japonica Tanaka, 1966 was described from one specimen of each sex and does not differ significantly from *B. palliata.* It is therefore regarded as a junior synonym. Tanaka's specimens were taken in a haul made between 1000–0m depth in the Pacific Ocean adjacent to the Izu region of Japan. This is the shallowest record of *B. palliata.*

Benthomisophria cornuta Hulsemann & Grice, 1964

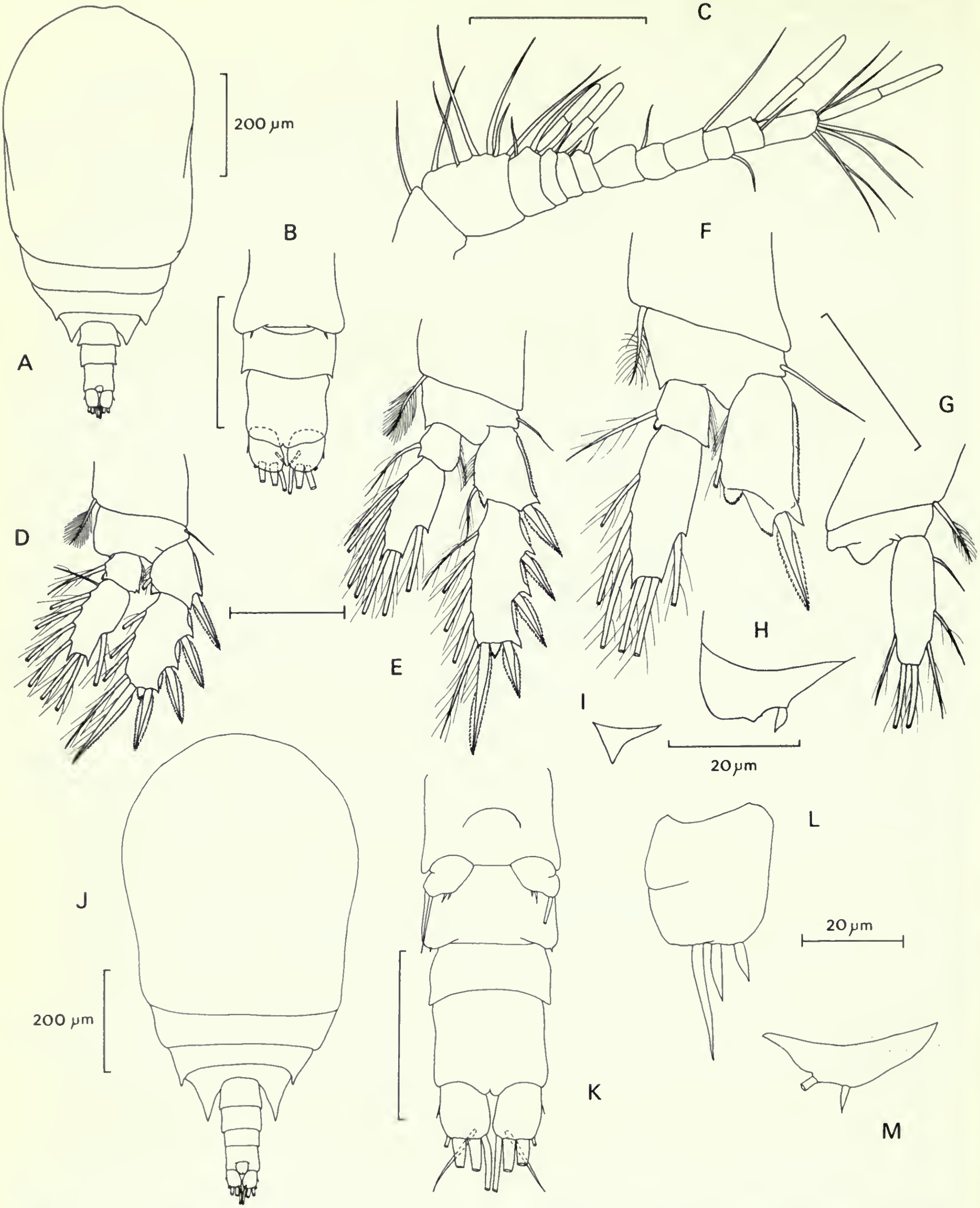
Benthomisophria cornuta K. Hulsemann & G. D. Grice, 1964: 259–260, Figs 1–15.
Misophria maculata. O. Tanaka, 1966: 55–56, Fig. 3.

The descriptions of the adults of both sexes and of the later copepodid stages of *B. cornuta* are based on the examination of a total of 40 specimens. The specimens were sorted, on morphological criteria, into copepodid stages III to V, adult male and adult female.

COPEPODID III

Prosome (Fig. 8A) large, 4-segmented, with the epimeral plates of the last two free thoracic somites produced posteriorly into acute projections. Urosome (Fig. 8B) 3-segmented; segments 1 and 2 bearing rudiments of legs 5 and 6 respectively. Caudal rami with 6 armature elements as in adult.

First antenna (Fig. 8C) 12-segmented; armature incomplete, elements present as follows: I – 1, II – 6, III – 2 + 1 aesthete, IV – 1, V – 1 + 1 aesthete, VI – 1 spine, VII – 0, VIII – 1, IX – 1, X – 1, XI – 1 + 1 aesthete, XII – 6 + 1 aesthete. Second antenna, labrum, mandible, maxillae and maxilliped as in adult.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K
M

Fig. 8 *B. cornuta* Copepodid III & IV. A, Copepodid III, dorsal; B, urosome, ventral; C, first antenna; D, leg 1; E, leg 2; F, leg 3; G, leg 4; H, leg 5; I, leg 6; J, Copepodid IV, dorsal; K, urosome, ventral; L, leg 5; M, leg 6. Scales 100µm unless otherwise indicated.

Legs 1 to 3 (Figs 8D–F) biramous, with 2-segmented rami; leg 4 (Fig. 8G) biramous with 1-segmented rami. Armature formula as follows:

	coxa	basis	endopod	exopod
leg 1	0 – 1	1 – 0	0 – 1 ; 1,2,5	I – 1 ; III,I,4
leg 2	0 – 1	1 – 0	0 – 1 ; 1,2,4	I – 1 ; III,I,5
leg 3	0 – 1	1 – 0	0 – 1 ; 1,2,3	I – 1 ; missing
leg 4	0 – 1	1 – 0	1,2,3	missing

All exopod segments bearing strips of serrated membrane laterally and all outer margin spines bilaterally serrate.

Leg 5 (Fig. 8H) a rounded process situated postero-laterally on first urosome somite, armed with a single rudimentary element subapically, another element may have been present but was missing from all specimens available for examination. Leg 6 (Fig. 8I) a small spinous process.

Body length ranging from 0·72 to 0·73mm, with a mean of 0·72mm (based on 3 specimens).

Copepodid IV

Prosome (Fig. 8J) large, comprising about 75% of total body length; epimeral plates of somites 3 and 4 strongly produced posteriorly. Urosome (Fig. 8K) 4-segmented.

First antenna (Fig. 9A) 15-segmented, with armature elements present as follows: I – 1, II – 11, III – 1 + 1 spine, IV – 2, V – 3 + 1 aesthete, VI – 1, VII – 1 + 1 aesthete, VIII – 2, IX – 1 + 1 spine, X – 1 (+ ?), XI – 1, XII – 1, XIII – 2, XIV – 1 + 1 aesthete, XV – 5 + 1 aesthete. Second antenna, labrum, mandible, maxillae and maxilliped as in adult.

Legs 1 to 4 (Figs 9B–E) biramous, with 2-segmented rami; armature formula as follows:

	coxa	basis	endopod	exopod
leg 1	0 – 1	1 – 0	0 – 1 ; 1,2,5	I – 1 ; III,I,4
leg 2	0 – 1	1 – 0	0 – 1 ; 1,2,5	I – 1 ; III,I,5
leg 3	0 – 1	1 – 0	0 – 1 ; 1,2,4	I – 1 ; missing
leg 4	0 – 1	1 – 0	0 – 1 ; 1,2,3	I – 1 ; missing

Leg 5 (Fig. 8L) a sub-rectangular plate, incompletely subdivided by a transverse suture line; distal margin with 3 armature elements. Leg 6 (Fig. 8M) a broad, flat process with 2 armature elements.

Body length ranging from 0·77 to 0·92mm, with a mean of 0·85mm (based on 7 specimens).

Copepodid V

Prosome (Fig. 9F) with epimeral plates on last two free thoracic somites strongly produced posteriorly; dorsal and lateral surfaces of prosome with reticulate surface markings as shown in Fig. 9G on the right hand lateral portion of the cephalosome. Urosome (Fig. 10A) 5-segmented; segments 1 to 4 with reticulate surface markings, segment 5 without surface markings.

First antenna (Fig. 10B) 16-segmented, with armature elements as follows: I – 1, II – 10, III – 9, IV – 2 + 1 aesthete, V – 2, VI – 2 + 1 aesthete, VII – 2, VIII – 2 + 1 aesthete, IX – 2, X – 2, XI – 2 + 1 aesthete, XII – 1, XIII – 1, XIV – 2, XV – 2 + 1 aesthete, XVI – 6 + 1 aesthete. Second antenna, labrum, mandible, maxillae and maxilliped as in adult.

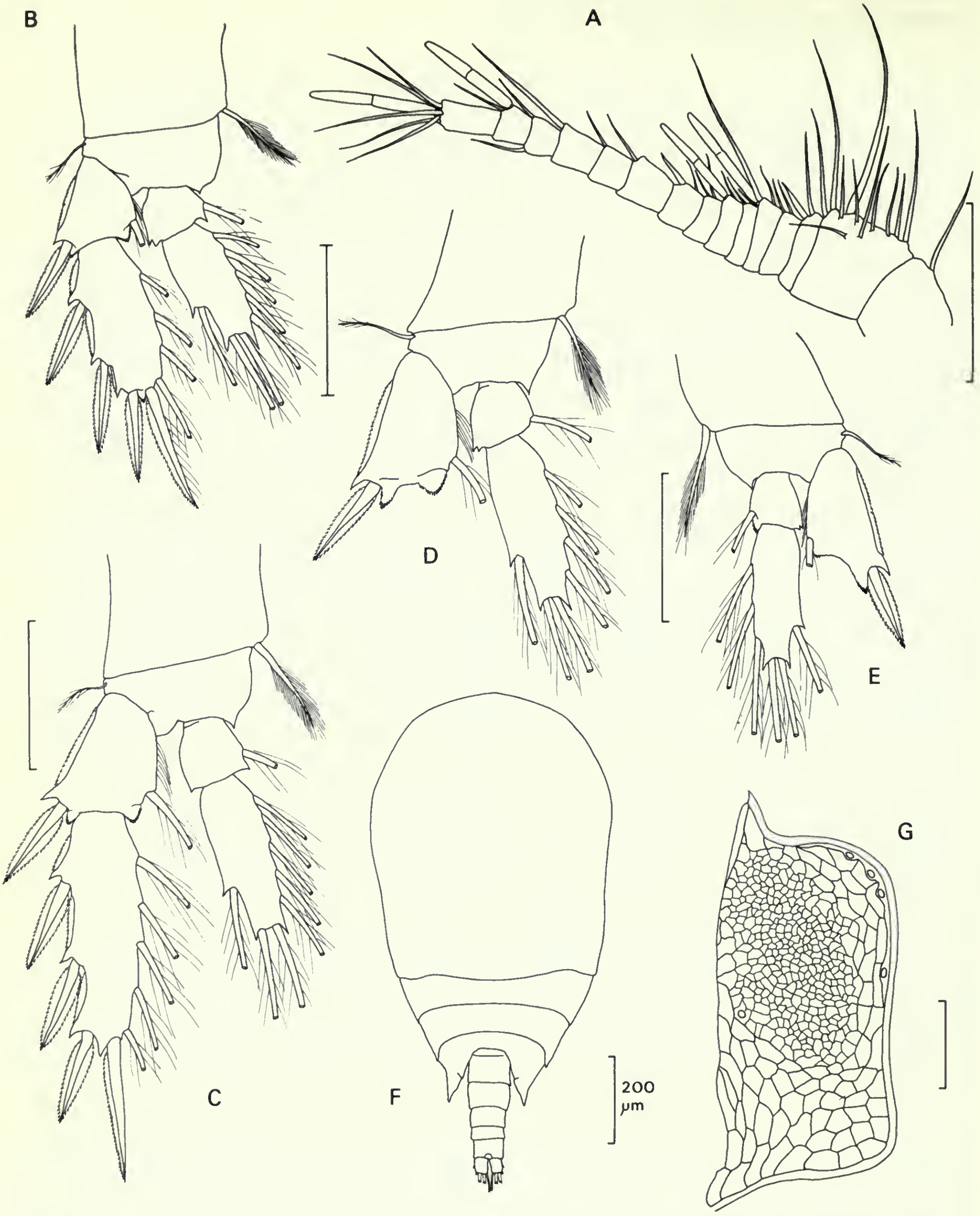

Fig. 9 *B. cornuta* Copepodid IV & V. A, Copepodid IV first antenna; B, leg 1; C, leg 2; D, leg 3; E, leg 4; F, Copepodid V, dorsal; G, lateral portion of cephalosome – showing reticulate surface markings. Scales 100µm unless otherwise indicated.

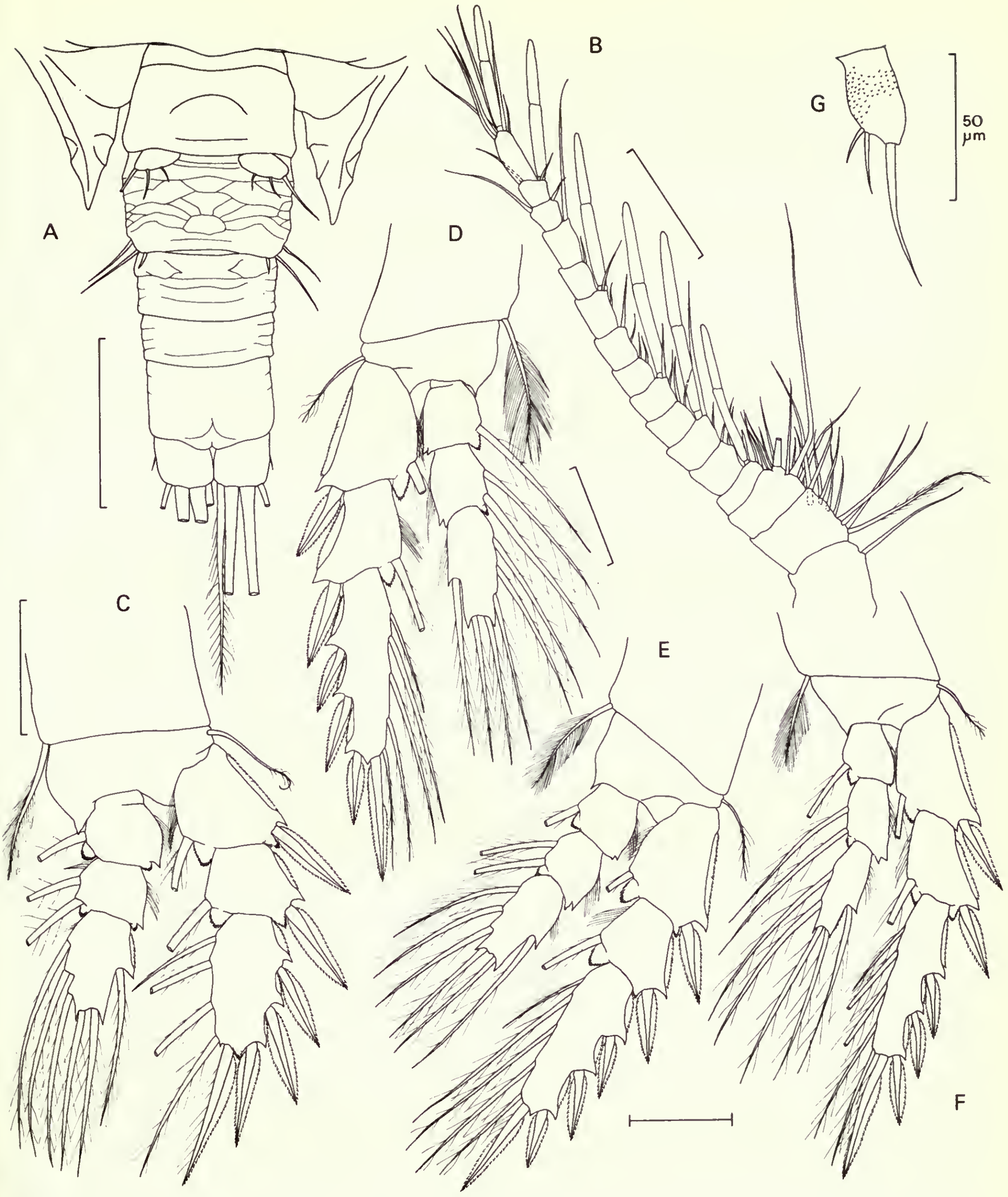

Fig. 10 *B. cornuta* Copepodid V. A, urosome, ventral; B, first antenna; C, leg 1; D, leg 2; E, leg 3; F, leg 4; G, leg 5. Scales 100µm unless otherwise indicated.

Legs 1 to 4 (Figs 10C–F) biramous, with 3-segmented rami; armature formula as follows:

	coxa	basis	endopod	exopod
leg 1	0 – 1	1 – 0	0 – 1 ; 0 –2 ; 1,2,3	I – 1 ; I – 1 ; III,I,4
leg 2	0 – 1	1 – 0	0 – 1 ; 0 –2 ; 1,2,3	I – 1 ; I – 1 ; III,I,5
leg 3	0 – 1	1 – 0	0 – 1 ; 0 –2 ; 1,2,3	I – 1 ; I – 1 ; III,I,5
leg 4	0 – 1	1 – 0	0 – 1 ; 0 –2 ; 1,2,2	I – 1 ; I – 1 ; III,I,5

Lateral margins of all endopod segments except segment 3 of leg 1 with rows of pinnules; lateral margins of endopod segment 3 of leg 1 and all exopod segments armed with strips of serrated membrane.

Leg 5 (Fig. 10G) a single segment, with no indication of any subdivision, armed with a long naked apical seta and 2 short naked setae distally on the medial margin; some denticulations also scattered over surface. Leg 6 (Fig. 10A) represented by 1 short and 2 long setae.

Body length ranging from 0·85 to 1·10mm, with a mean of 1·0mm (based on 10 specimens).

ADULT MALE

Prosome (Fig. 11A) 4-segmented; epimeral plates of last two free thoracic somites strongly produced posteriorly; lateral indentations present on cephalosome (as in all other stages) allowing for movement of setae on mandibular palp and second antenna. Prosome with conspicuous reticulate surface markings both dorsally and laterally. Urosome (Fig. 11B) 6-segmented; segments 1 to 5 with reticulate surface markings, segment 6 without surface markings.

First antenna (Fig. 11D) apparently 16-segmented; geniculate,with articulation between segments XIV and XV; aesthetes present on segments I, II (2), III, V (2), VIII, IX, XI, XIII, XV and XVI (2); segment XV also with a long spiniform process originating near base of aesthete; other armature elements omitted from basal region in Fig. 11D for greater clarity. All other appendages as in adult female.

Body length of males ranging from 1·06 to 1·37mm, with a mean of 1·23mm (based on 6 specimens).

ADULT FEMALE

Prosome (Fig. 11G) 4-segmented, epimeral plates of last two free thoracic somites strongly produced posteriorly; surface of prosome with conspicuous reticulate surface markings (not figured) extending onto rostrum and labrum (Fig. 11C). Major reticulations on prosome divided into minute networks of fine markings, as shown on rostrum (Fig. 11C). Urosome 6-segmented, segments 1 to 5 with reticulate surface markings, segment 6 without markings.

Labrum (Fig. 11C) strongly developed, fused to rostrum; projecting postero-ventrally from ventral body surface, and with reticulate markings on ventral surface.

First antenna (Fig. 12A) 16-segmented; armature elements present as follows: I – 1, II – 9, III – 5, IV – 1 + 1 spine + 1 aesthete, V – 1, VI – 1 + 1 aesthete, VII – 0, VIII – 2 + 1 aesthete, IX – 1, X – 1, XI – 1 + 1 aesthete, XII – 1, XIII – 0, XIV – 2, XV – 2 + 1 aesthete, XVI – 7 + 1 aesthete.

Second antenna (Fig. 12B) basis with 1 outer distal seta; endopod 3-segmented and exopod with 5 distinct segments and possibly a sixth fused to basis. Endopod segment 1 unarmed, segment 2 with 4 outer margin setae, segment 3 with 1 outer margin seta and 6 long plumose apical setae. Exopod with 1 seta on each of first 4 distinct segments and with 3 setae on terminal segment.

Mandible (Fig. 12C) blade armed with 5 main teeth, 3 hirsute setae and a naked seta; mandibular palp biramous, with a 2-segmented endopod and 4-segmented exopod; endopod segments 1 and 2 bearing 2 and 6 setae respectively; exopod segments 1 to 4 bearing 2,1,1 and 2 long plumose setae respectively.

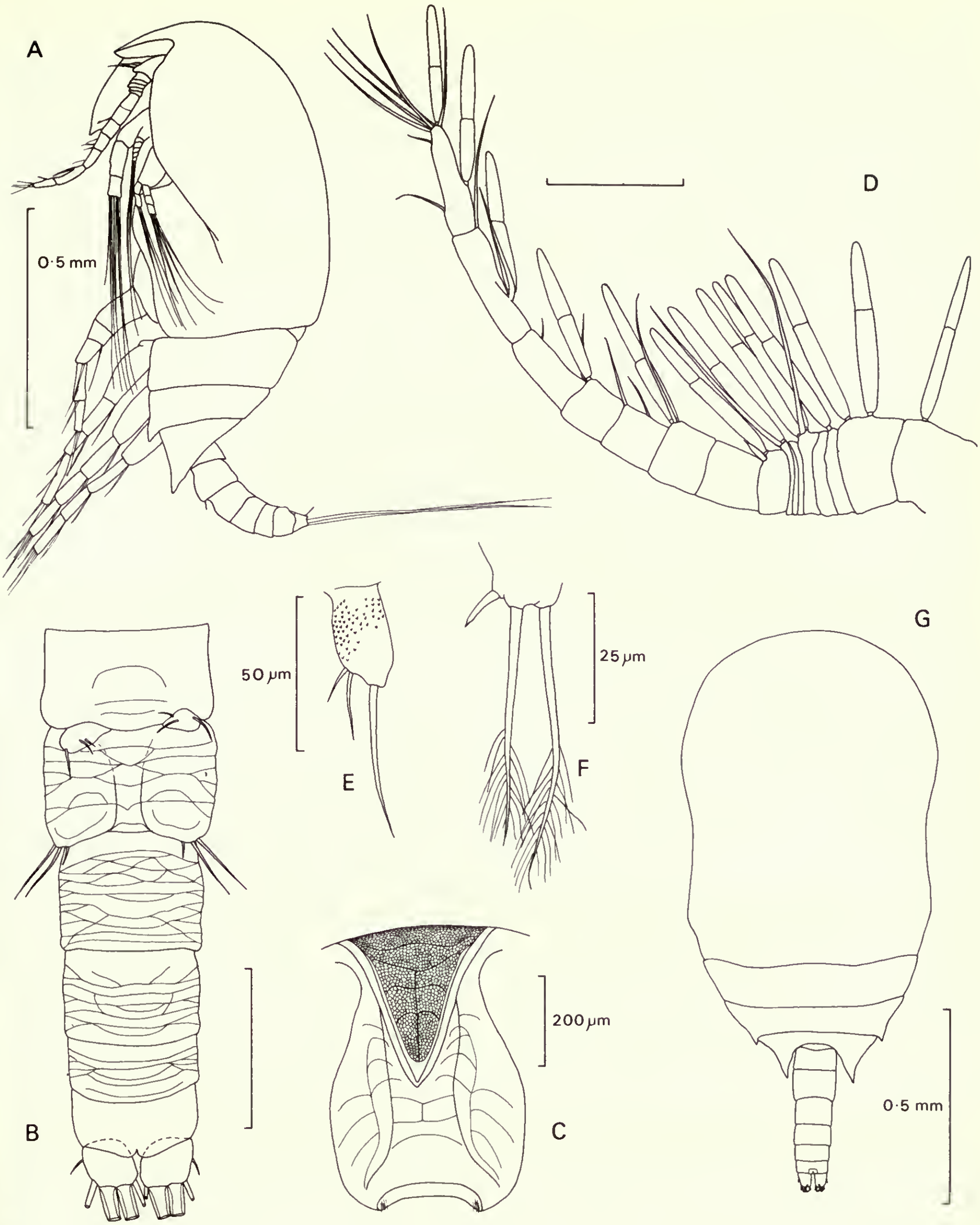
A
0·5 mm
D
B
50 µm
E
25 µm
F
G
200 µm
C
0·5 mm

Fig. 11 *B. cornuta* Adult male and female. A, Male, lateral; B, urosome, ventral; C, Female labrum, ventral; D, Male first antenna (with setae omitted from proximal portion); E, Female leg 5; F, leg 6; G, Female, dorsal. Scales 100µm unless otherwise indicated.

First maxilla (Fig. 12D) gnathobase with 15 armature elements; inner lobes 1 and 2 with 5 and 4 setae respectively; outer lobe rudimentary, represented by 6 plumose setae on surface of segment; endopod apparently 2-segmented with small distal segment positioned at an angle of 90° to proximal segment, proximal segment with 4 setae apically, distal segment with 2 naked setae medially and 1 naked and 2 plumose setae apically; exopod large, 1-segmented, with 6 plumose setae apically and 3 naked setae subapically on medial margin.

Second maxilla (Fig. 12E) apparently 6-segmented; first segment with proximal inner lobe bearing 4 plumose setae and distal inner lobe with 3 plumose setae; second segment with 2 inner lobes, each bearing 3 distal setae; third segment produced medially into a strong, slightly curved claw armed with 2 slender naked setae basally; distal 3 segments bearing a total of at least 8 elements.

Maxilliped (Fig. 12F) 5-segmented; first segment with 1 small naked seta and 2 plumose setae proximally and 2 plumose setae distally on medial margin; second segment with 3 plumose setae on medial margin; third segment small, bearing 1 seta; fourth segment with 4 setae; fifth segment reduced, armed with 5 setae.

Legs 1 to 4 (Figs 13A–D) biramous, with 3-segmented rami; armature formula as follows:

	coxa	basis	endopod	exopod
leg 1	0 – 1	1 – 0	0 – 1;0 –2;1,2,3	I – 1;I – 1;III,I,4
leg 2	0 – 1	1 – 0	0 – 1;0 –2;1,2,3	I – 1;I – 1;III,I,5
leg 3	0 – 1	1 – 0	0 – 1;0 –2;1,2,3	I – 1;I – 1;III,I,5
leg 4	0 – 1	1 – 0	0 – 1;0 –2;missing	I – 1;I – 1;missing

Pinnule rows present on lateral margins of all endopod segments and medial margins of exopod segments; lateral margins of all exopod segments and of endopod segment 3 of leg 3 armed with strips of serrated membrane; all outer margin spines bilaterally serrate, apical spine on exopods of legs 2 and 3 bilaterally serrate, that on leg 1 unilaterally serrate.

Leg 5 (Fig. 11E) 1-segmented, without trace of suture line; armed with 1 long naked apical seta and 2 short subapical setae on medial margin; denticulations scattered over surface of segment. Leg 6 (Fig. 11F) a simple process bearing 2 plumose setae on distal margin and a short spine at the disto-medial angle.

Body length of female ranging from 1·18 to 1·33mm, with a mean of 1·25mm (based on 9 specimens).

MATERIAL EXAMINED

Holotype ♀; *Discovery* Stn 4768 (40°03′N 19°57′W), BM(NH) registration number 1964.7.10. Hulsemann and Grice, 1964.

10♀♀, 6♂♂, 11 Co.V, 9 Co.IV, 4 Co.III; *Discovery* Stns 9541 and 9131 (see Table 3); BM(NH) registration numbers 1979.71–80 (♀♀), 1979.81–86 (♂♂), 1979.87–97 (Co.V), 1979.98–106 (Co.IV) and 1979.107–110 (Co.III).

REMARKS

Hulsemann & Grice (1964) described the first antenna of this species as being 17-segmented, with the apical segment very small. The first antenna of the holotype on the prepared slide of the appendages (BM(NH) No. 1964.7.10) appears to have a seventeenth segment but examination of the other first antenna of the pair (figured in Fig. 12A) shows that the seventeenth segment of Hulsemann & Grice is actually the base of the apical aesthete and that this appendage is only 16-segmented.

This species is readily distinguishable from *B. palliata* on the basis of its small size, distinctive surface ornamentation, prolonged epimeral plates on the last 2 free thoracic somites, leg 5 and the segmentation of the first antenna.

There are no significant differences between *B. cornuta* and *Misophria maculata* Tanaka,

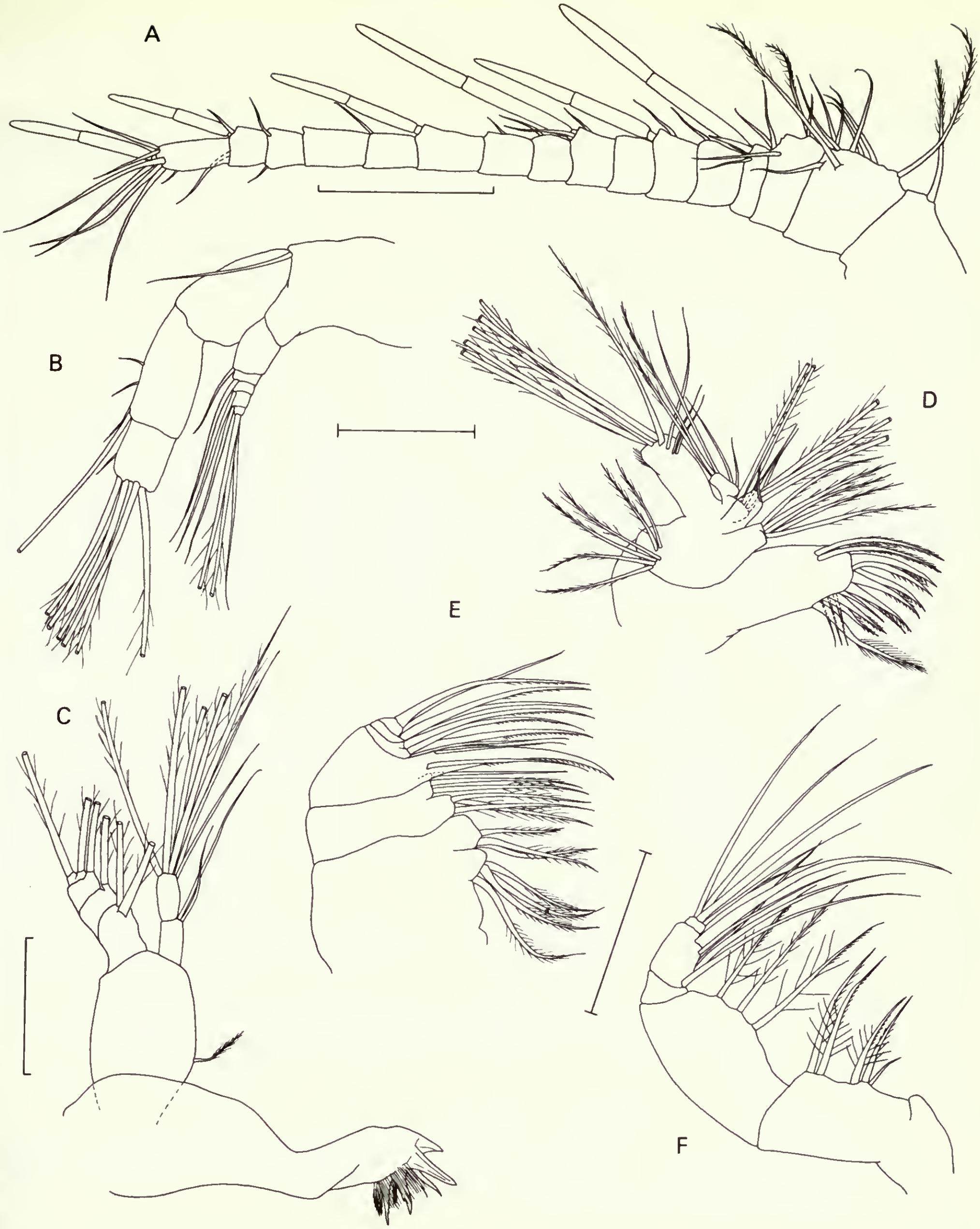

Fig. 12 *B. cornuta* Adult female. A, Holotype ♀ (BM(NH) Reg. No. 1964.7.10), first antenna; B, Female second antenna; C, mandible; D, first maxilla; E, second maxilla; F, maxilliped. Scales 100µm.

1966. The slight differences between them can be accounted for largely by missing or damaged armature elements. *M. maculata* is therefore regarded as a junior synonym of *B. cornuta.* Tanaka's single female specimen was taken in a haul made between 1000–0m depth in the Pacific Ocean adjacent to the Izu region of Japan. This is the shallowest record of *B. cornuta.*

Genus *MISOPHRIA*

Misophria pallida Boeck, 1864

Misophria pallida A. Boeck, 1864: 248.

Gurney (1933) collected ovigerous female *M. pallida* and successfully hatched the eggs from them. He described the nauplius and copepodid I stages of this species. The descriptions given below are based on Gurney (1933).

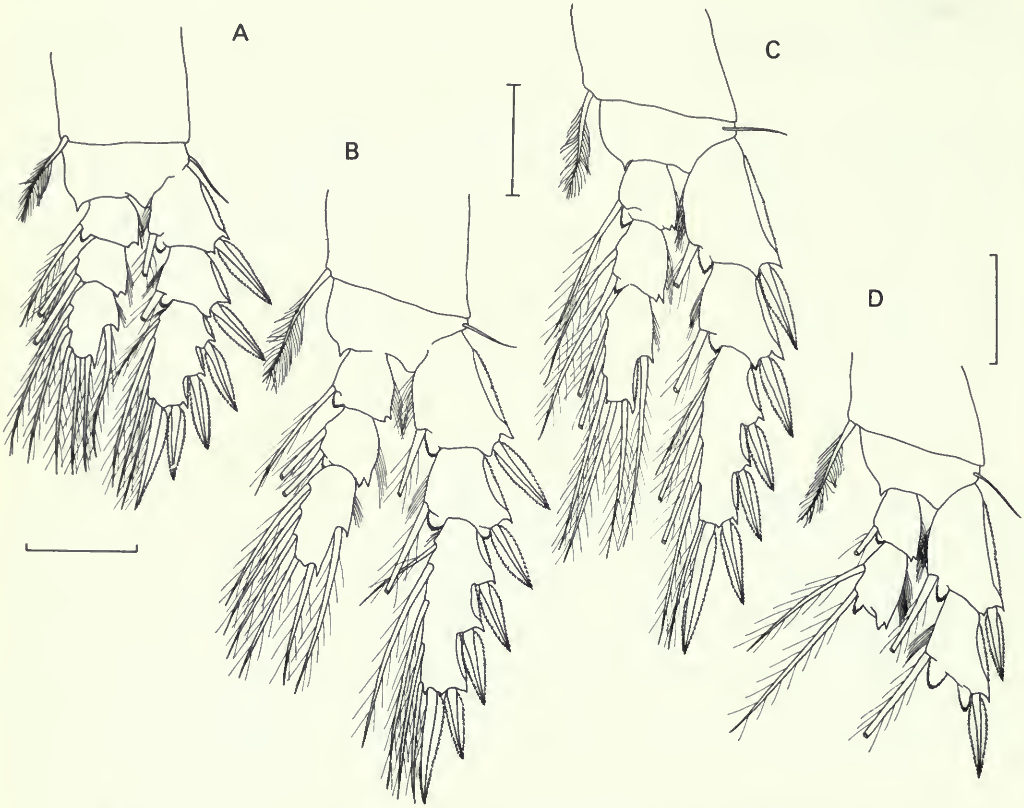

Fig. 13 *B. cornuta* Adult female. A, leg 1; B, leg 2; C, leg 3; D, leg 4. Scales 100µm.

NAUPLIUS

Body rounded anteriorly, with maximum width at level of mandible. Eye absent. Mouth absent. Body filled with yolk. Appendages without gnathobases. First antenna uniramous and 2-segmented. Second antennae and mandibles biramous, with 4-segmented exopods. Rudiments of legs 1 and 2 visible through cuticle.

COPEPODID I

Body apparently as in *Benthomisophria palliata* copepodid I. Urosome 1-segmented. Caudal rami with 6 setae. First antenna 6-segmented. Labrum large. Second antenna, mandibles, first and second maxillae and maxillipeds present and similar in structure to those of the adult. Legs 1 and 2 biramous, with 2-segmented sympods and 1-segmented rami; armature formula for rami as follows:

	endopod	exopod
leg 1	1 , 2 , 4	IV , I , 3
leg 2	1 , 2 , 2 (or 3?)	III , I , 2

Leg 3 a broad flattened structure, bilobed distally, bearing 2 small apical setae on outer lobe; inner lobe apparently unarmed. Leg 4 rudimentary, comprising a spinous process on a broad base.

REMARKS

The adult male and adult female are described in detail by Sars (1903). The similarities between the Copepodid I and the adult stages of *Misophria pallida* and *Benthomisophria palliata* suggest that development in these two genera follows a similar pattern through the copepodid stages. The nauplius of *Benthomisophria* is unknown but it may well resemble the yolky nauplius of *Misophria.*

Development in the Misophrioida appears to be characterized by only a single nauplius stage remaining in the life cycle. The yolk-filled non-feeding nauplius is short lived in *M. pallida,* moulting into the Copepodid I stage within about a day (Gurney, 1933). A similar type of lecithotrophic nauplius is found in many associated or parasitic copepods belonging to the orders Siphonostomatoida, Poecilostomatoida and Cyclopoida. The lecithotrophic nauplii possess more simply constructed appendages than those of the nauplii of free-living forms (Dudley, 1966). The lecithotrophic nauplius may represent an apomorphic character state, derived independently in several copepod orders as an adaption to an associated or parasitic mode of life. The adaptive significance of the presence of a single lecithotrophic nauplius in the life cycle of *M. pallida* (Misophrioida) will remain unknown until more data on the feeding biology and ecology become available for this species.

Variation

Body length

All the complete specimens of *B. palliata* were measured (Table 2) and the body length frequency distributions were calculated for all stages (Figs 14 & 15). The size range for each stage is extremely wide. In both adults and in the later copepodid stages the frequency distributions appear to be bimodal, indicating that two size groups are present within the population.

In the Copepodid V the modes are at 2·28 (2·24–2·32) and 2·96 (2·92–3·00)mm, in the adult male at 3·22 and 3·97mm and in the adult female at 3·30 and 4·35mm. There also appear to be traces of similar bimodality in the preceding copepodid IV and III stages, but more data are required to confirm this pattern. If the existence of a bimodal distribution at each stage from Copepodid III onwards is accepted, modes can be recognized at 1·22 and 1·52mm (Co.III), 1·75 and 2·05mm (Co.IV), 2·28 and 2·96mm (Co.V), 3·22 and 3·97mm (male) and 3·30 and 4·35mm (female). The proportional increase in body length from one stage to the next (for example, Co.III to Co.IV, or Co.V to female) of the small and/or the large form varies from 1·30 to 1·47 for each moult. These results indicate that the small and large size morphs persist from one moult to the next and, therefore, that a small Co.V would moult into a small adult male or adult female.

The small and large morphs differ only in size, no other morphological differences were observed between them. There is also a difference in the vertical distribution of the two morphs (page 37).

Body shape

In addition to size dimorphism there is also considerable variation in the body shape of *B. palliata* individuals. Some specimens have a bloated, inflated appearance whereas others are much thinner. Swollen specimens are inflated both laterally and dorsally and have a distinct hump-backed appearance in lateral view (Figs 16D–E). Slim individuals have a much flatter dorsal profile (Figs 16B–C).

These changes in body proportions occur in both small and large individuals and do not correspond to changes in body length. In all other aspects of external morphology individuals of both types are identical. The gut, however, is very distended in swollen specimens

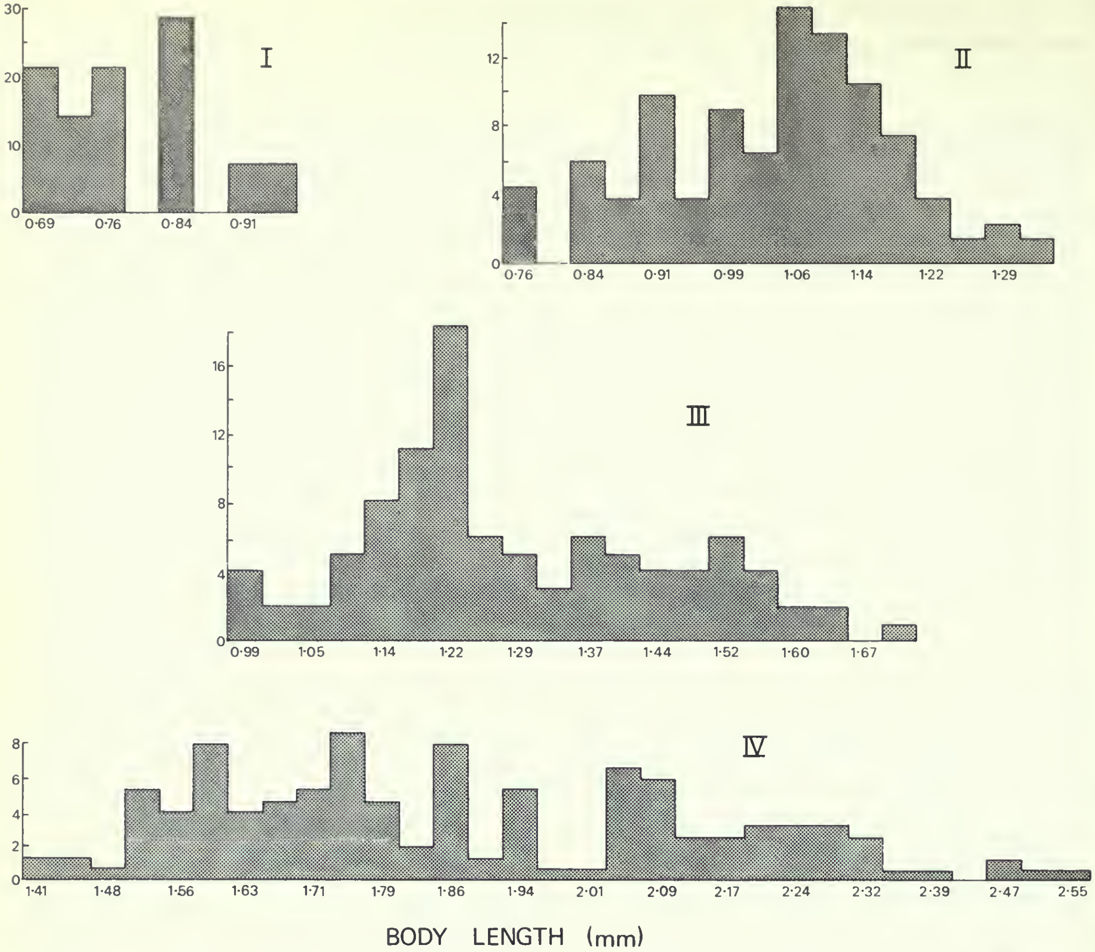

Fig. 14 Size frequency distribution (in percent) of *B. palliata* Copepodid I – IV stages, using data from all measured specimens (see Table 2).

and is visible through the thin carapace virtually filling the entire prosome (Figs 16D–E). In slim individuals the gut is much smaller and cannot be seen through the carapace (Figs 16B–C).

The gut comprises a thin walled tube which is relatively wide in the prosome and is constricted just before entering the urosome. There is an anterior lobe extending into the head and two lateral lobes. In swollen individuals the gut is usually full (Figs 16F–G), in slim individuals it is empty (Fig. 16A). The gut contents are mainly small copepods, with a substantial amount of unidentifiable residue, mostly in the form of convoluted strings of tissue. The latter are possibly the remains of chaetognaths or coelenterates. A single radiolarian was also found.

The combination of a very elastic gut and a thin flexible integument enables *B. palliata* to gorge until its entire prosome is distended. The ornate pattern of surface markings on the exoskeleton of this species may facilitate this stretching. A similar gorging phenomenon has been observed in some species of abyssal amphipods (Shulenberger & Barnard, 1976, Thurston, 1979) and in the leptostracan *Nebaliopsis typica* (Rowett, 1943, Cannon, 1946). The ability to eat as much as possible when the opportunity arises is presumably a considerable advantage in areas, such as deep oceans, where food is scarce.

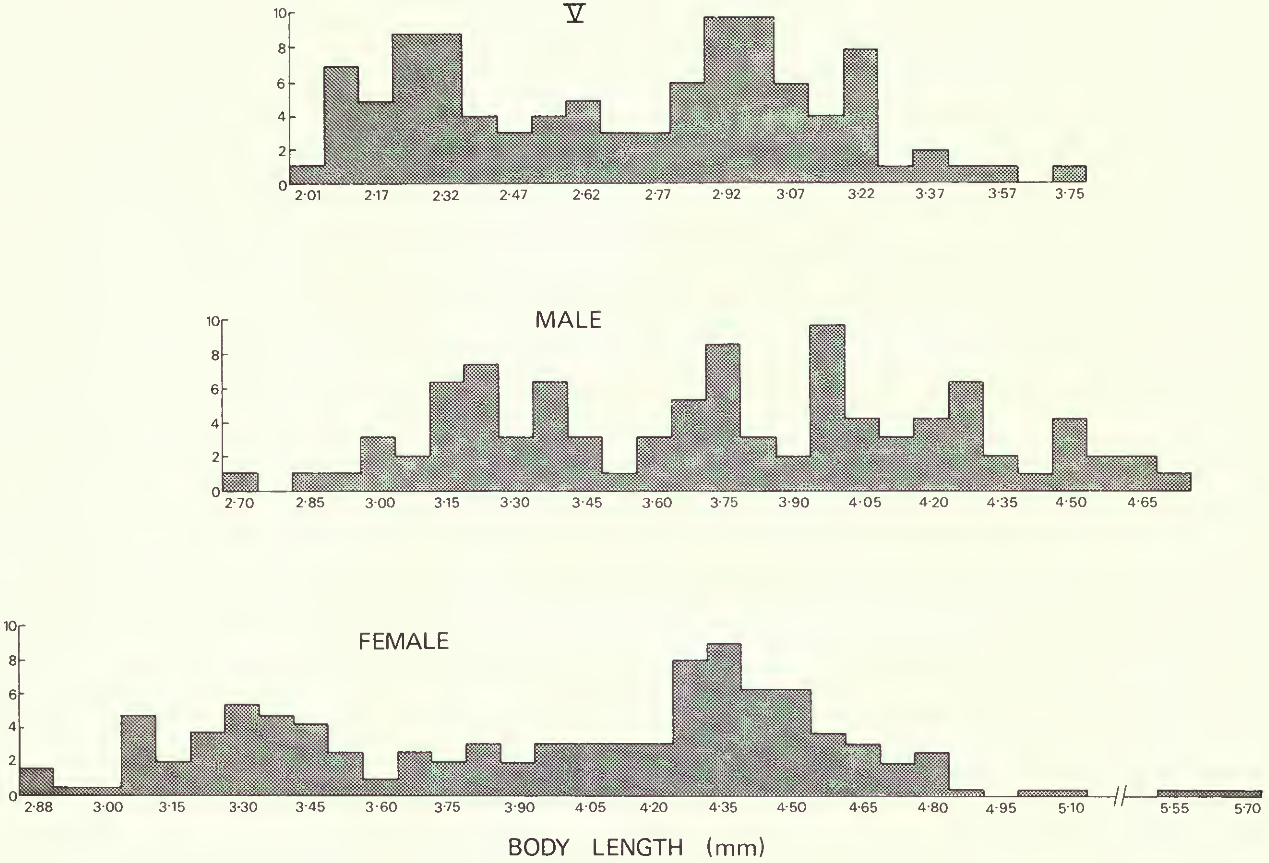

Fig. 15 Size frequency distribution (in percent) of *B. palliata* Copepodid V and adults, using data from all measured specimens (see Table 2).

Similarly it is advantageous in such situations to be able to accurately locate a food supply. There is some evidence (Thurston, 1979) that copepods were attracted to a baited fish trap laid in a water depth of 4885m. The numerous large aesthetes on the first antennae of *B. palliata* probably have a chemosensory function. A chemosensory system will be necessary for the location of food in all post-naupliar stages. The large number of aesthetes on the first antennae of the adult male suggests that they also have a reproductive function, possibly enabling the male to locate a female. Other male copepods have been shown to respond to sex pheromones produced by the females, thereby demonstrating the existence of a chemosensory system (Katona, 1973).

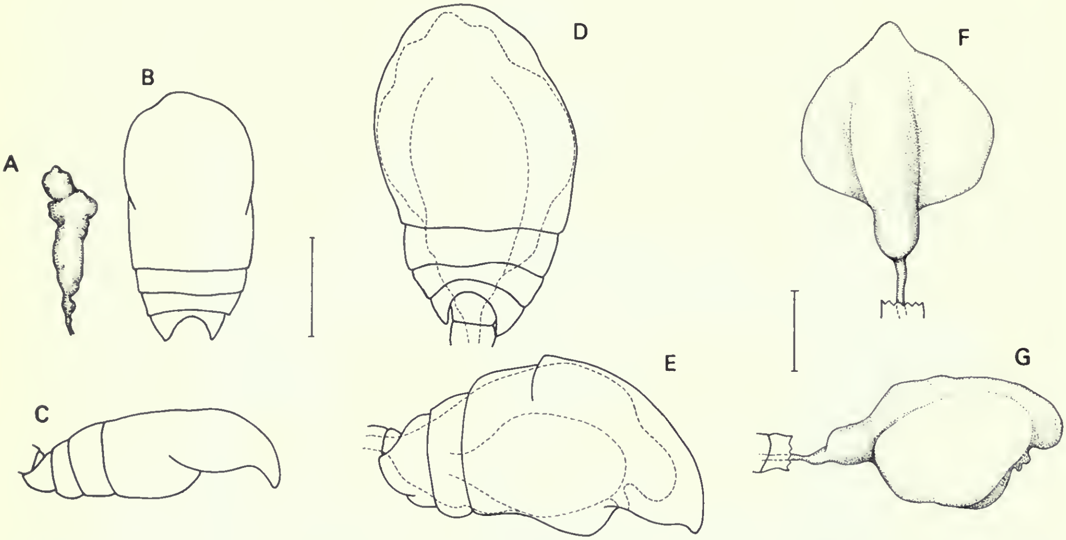

Fig. 16 Variation in body shape in *B. palliata*. Slim specimen (♂ T.L. 3·22mm, Stn 9541 # 18) A, gut; B, prosome, dorsal; C, prosome, lateral. Swollen specimen (♀ T.L. 4·27mm, Stn 9541 # 18) D, prosome, dorsal; E, prosome, lateral – both with gut visible through body wall. Swollen specimen. (♀ T.L. 4·5mm, Stn 9541 # 22) F, gut, dorsal; G, gut, lateral. Scales 1mm.

Vertical distribution

Benthomisophria palliata

The vertical distributions of the copepodid and adult stages of *B. palliata* caught in the RMT 1 series at Station 9541 are shown in Figure 17. The two hauls that fished between 5–20m off the bottom (# 18 and 19, Table 1) have been combined, and as there was no sexual difference in distribution the adults have also been combined. *B. palliata* is too small to be adequately sampled by the RMT 8 and the Copepodid I and II stages, with mean body lengths of 0·79 and 1·03mm respectively, are probably not taken effectively by the RMT 1 either. The results from the RMT 1 series at Station 9131 are similar to those for Station 9541 but this series was incomplete. The numbers of specimens in each haul have been corrected for an equal volume of water filtered.

The depth range of all stages is very wide, extending from 2500m to the bottom. In addition, a single adult was caught between 2000 and 2500m. There are no apparent differences in depth distribution between the various stages or between the sexes. At no depth is the species abundant, but there is a general increase in numbers in the deepest samples taken within 500m of the bottom. After correction for the volume of water filtered, the greatest number of specimens caught in a single haul (all stages combined) was 136, in the 5–20m off the bottom sample. Assuming an even distribution this represents 1 animal per 106m^3 of water. The largest number of any particular stage caught was 45 adults, also in the 5–20m sample. This represents 1 animal per 322m³. In terms of biomass these figures are infinitesimal.

The mean body length at each depth of each stage of *B. palliata* was calculated, using the same RMT 1 series of hauls from Station 9541 (Fig. 18). The mean length of each copepodid stage is more or less uniform throughout the depth range. Both males and females, however, are apparently larger in the samples taken within 500m of the bottom.

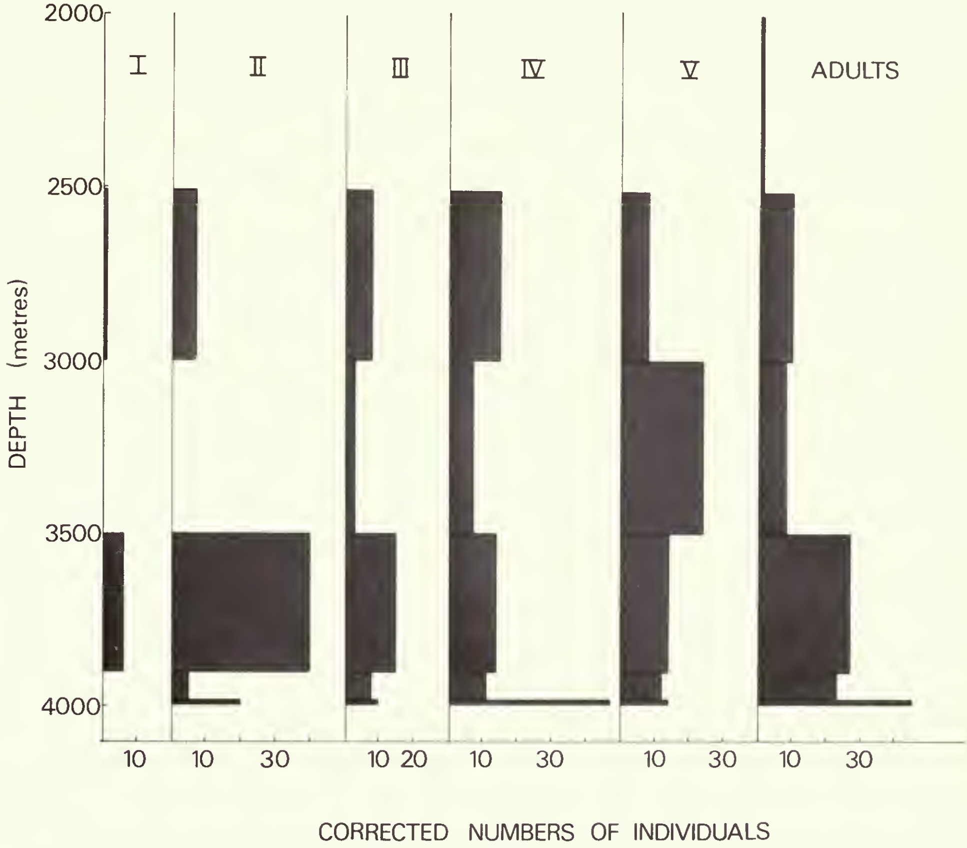

Fig. 17 Vertical distributions of the Copepodid and adult stages of *B. palliata*, based on RMT 1 series at Station 9541.

Some stages (Co. V, ♂ and ♀) show distinct large and small size morphs (page 33). In Co. V stage both small and large morphs occur throughout the depth range. In the adults small morphs are found at all depths but large ones are not. Females longer than 3·67mm and males longer than 3·45mm in total body length were found only in the deepest hauls taken within 500m. of the bottom. It is, therefore, only this deep population that shows the total range in body length and the bimodal size frequency distribution (Figs 14 & 15).

Benthomisophria cornuta

The numbers of *B. cornuta* caught in each haul are shown in Table 3. These numbers are insufficient to permit detailed analysis and it is likely that the RMT 1 does not effectively sample the copepodid stages of this small species.

The catch data suggest that, as with *B. palliata*, the vertical range occupied by this species is very wide, extending from 2500m to the bottom.

Phylogenetic relationships

The order Misophrioida comprises two genera, *Misophria* and *Benthomisophria,* and three species *M. pallida, B. palliata* and *B. cornuta.* The species and genera are most clearly separated on the basis of the segmentation of the leg 5. In *Misophria pallida* the leg 5 consists of 3 distinct segments. In *Benthomisophria palliata* the leg 5 is 2-segmented. The basal segment is notched laterally and bears a small suture line indicating that it probably represents two incompletely fused segments, derived from the 3-segmented type of leg 5 found in *M. pallida.* In *B. cornuta* the process of fusion of the segments has progressed further and the leg 5 is 1-segmented in the adult. The condition found in the Copepodid IV stage of this species (Fig. 8L) suggests that the single segment is derived from the fusion of two distinct segments.

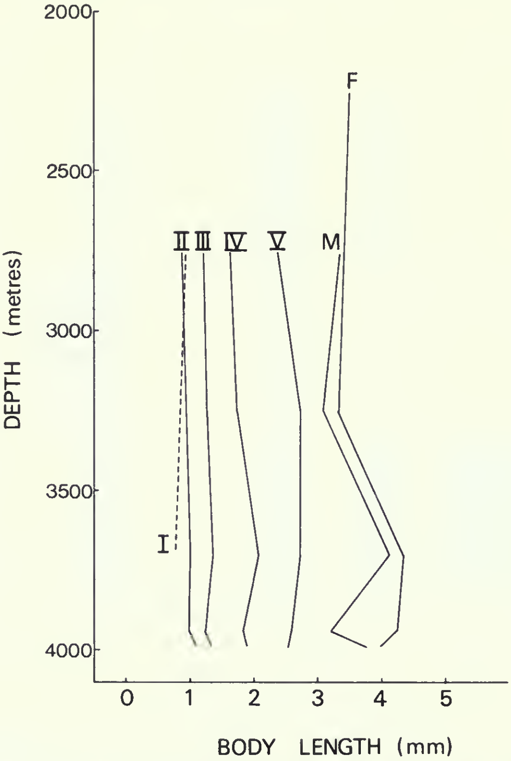

Fig. 18 Mean body length, at each depth, of the Copepodid stages and the adult male (M) and female (F) of *B. palliata.* (Copepodid I line is hatched). Based on data from RMT 1 series at Station 9541.

There appears to be a phylogenetic transformation series from the plesiotypic 3-segmented condition, via the intermediate 2-segmented condition, to the apotypic 1-segmented condition. The cladogram (Fig. 19) shows the probable phylogenetic relationships between the 3 species included in the Misophrioida.

Hulsemann & Grice (1964) reviewed the historical aspects of the classification of the Family Misophriidae within the Copepoda. *Misophria* has long been recognized as representing a distinct group within the Copepoda. Giesbrecht (1892) placed *Misophria* in a separate family, the Misophriidae and, according to Gurney (1927), Giesbrecht's families are now largely regarded as equivalent to orders. Gurney (1933) proposed that *Misophria* should be regarded as the type of a separate order, the Misophrioida. Lang (1948) erected the suborder Propodoplea, to contain the family Misophriidae. In a recent work on the classification of the Copepoda, Kabata (1979) regarded the Misophrioida as an early offshoot from the podoplean line and this system has been adopted in the present account.

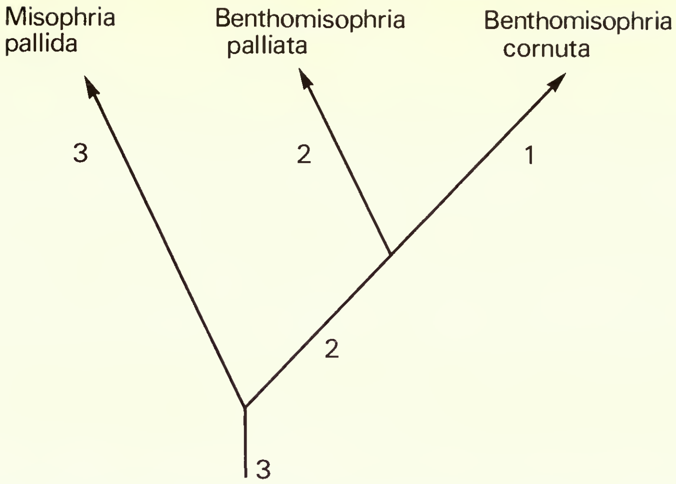

Fig. 19 Cladogram showing the probable phylogenetic relationships between the three species comprising the Misophrioida. (1,2 or 3 denotes the number of segments in the adult leg 5).

Discussion

The samples analysed are the first to have been taken close to the bottom in the total water column programme initiated by the Instiue of Oceanographic Sciences in 1976. The new near-bottom sampling technique employs bottom indicator switches that are rather inaccurate and difficult to use. A near bottom echo sounder is being developed to facilitate this type of sampling.

B. palliata has rarely been caught but it has a wide geographical distribution. It was recorded by Sars (1909) from 3 stations in the northeastern Atlantic in hauls made with open nets fished from depths of 2585 (also given as 5285m), 1414 and 3465m. Tanaka (1966) found a single specimen of each sex between 1000–0m depth in the Pacific adjacent to the Izu region of Japan. The present material extends its geographical range southwards in the eastern North Atlantic.

B. palliata has not previously been caught with closing nets. The new data indicate that *B. palliata* is bathypelagic but that its vertical distributions show little affinity with the sea bottom. It occupies a wide depth range and has no well defined optimum depth. Sars' (1909) specimens were presumably caught in the deep parts of his tows and Tanaka's (1966) record is the shallowest of this species.

Only two specimens of *B. cornuta* have been recorded, both female. One was taken in the northeastern Atlantic at 40°03·5′N 19°57′W, between 4750 and 4000m depth (Hulsemann & Grice, 1964), and the other off Izu, Japan between 1000–0m (Tanaka, 1966 – as *M. maculata*). The present record extends the known geographical of *B. cornuta* southwards in the North Atlantic. Too few specimens were taken to clarify its vertical distribution but it seems similar to that of *B. palliata,* with a wide depth range.

The analysis of body length frequency distribution in *B. palliata* indicated that two size morphs of *B. palliata* were present in the population. There was a slight difference in the vertical distribution of the two morphs in the adults of both sexes but there were no other morphological differences. This kind of size dimorphism has been observed in several other planktonic copepods, such as *Oncaea venusta* Philippi, 1843 (Boxshall, 1977). The explanation of this dimorphism must await additional seasonal, geographical and ecological data.

The ability to gorge and distend the body wall when the opportunity arises has now been found in three distinct crustacean groups, as well as in several midwater fish (Murray & Hjort, 1912). In *Benthomisophria* and the amphipod *Paralicella* Chevreux, 1908 the gut is very elastic but has no other obvious structural modification. *Nebaliopsis typica* G. O. Sars, 1887 is specialized in having a very distensible mid gut sac (Rowett, 1943). When this is filled the cephalothorax is so distended that its posterior region protrudes behind the carapace (Cannon, 1931 & 1946). *N. typica* is bathypelagic and is believed to feed by sucking eggs. The mid gut sac is presumed to be a storage organ enabling the animal to take maximum advantage of an irregular food supply (Rowett, 1943; Cannon, 1946). Except for the amphipods all the animals that are known to have the ability to gorge live in midwater at depths where food items are likely to be scarce. It is perhaps to be expected that modifications to enable opportunistic feeding exist in such an environment. Bottom living animals possibly have a more continuous supply of food available to them, both from the benthic community and from the 'rain' of debris. The ability to utilize infrequent large particles of food is, however, clearly advantageous and *Paralicella* is adapted accordingly.

Acknowledgements

Mr M. J. Harris and Mr R. Wild devised and made the bottom indicator switch system. Mr A. de C. Baker drew the bathymetric chart and plotted the net tracks. We would also like to thank Mr P. M. David and Dr R. J. Lincoln for stimulating discussion of the paper. Dr G. Testa of the Musée Océanographique de Monaco kindly arranged the loan of the *B. palliata* material from the S.A.S. *Le Prince Albert de Monaco.*

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Abyssal benthic Amphipoda (Crustacea) from the East Iceland Basin

1. The genus *Rhachotropis*

Michael H. Thurston K
Institute of Oceanographic Sciences, Wormley, Godalming, Surrey

Introduction

Cruise 39 of R.R.S. *Discovery,* made in April-June 1971, was concerned with biological projects in the north-east Atlantic Ocean. Major programmes involved intensive investigations of the vertical distribution and diurnal migration of planktonic and nektonic organisms at 60°N 20°W and 53°N 20°W. As an adjunct to the midwater work at the northern station, five hauls were made with a large epibenthic sledge at depths of 2600–2800m on the floor of the East Iceland Basin.

The present paper, describing species of the eusirid genus *Rhachotropis,* is the first to deal with the 120 species of gammaridean amphipods recovered from these benthic samples.

A considerable body of data is available on the bathyal and abyssal gammarid amphipods of the temperate north Atlantic Ocean. Among the more important contributions are those of Bonnier (1896), Chevreux (1900, 1927, 1935), Stephensen (1915, 1923, 1925, 1931, 1944*a*) and Mills (1967, 1971). Evidence summarized by Briggs (1974: 390) suggests that the bathyal and abyssal fauna of the Greenland and Norwegian Seas (and the Arctic Basin as a whole) is fairly distinct from that of the North Atlantic, but data on the deep-dwelling amphipods of these areas are relevant to the present study. Major works are those of Boeck (1876) and Sars (1885). Regional studies dealing mainly with shallow water faunas, but including data on slope species include the works of Sars (1890–1895), Stephensen (1933, 1935, 1938, 1940*a, b,* 1942, 1944*b*) and Gurjanova (1951).

The past twenty years have seen an upsurge in interest in the fauna of the deep sea. Investigations have shown that the bathyal and abyssal biomass is, in general, lower by several orders of magnitude (see, for example, Zenkevitch, 1963: 723) than that of the continental shelf and upper continental slope. Despite the low biomass, the number of species represented is frequently high (see, for example, Barnard (1962), Menzies (1962), Sanders *et al* (1965)), so much so that the species diversity is higher at these depths than in many other shallower and more productive marine environments (Hessler & Sanders (1967), Sanders (1968)). The nature and causes of high diversity have been discussed by Sanders (1969), Sanders & Hessler (1969), Dayton & Hessler (1972) and Grassle & Sanders (1973).

The collecting effort which has been devoted to sampling the deep sea benthos in recent years has made available large quantities of biological material. Problems of sorting and identification of organisms has led to much of this material being studied in general terms only, identification being made to phylum, class or perhaps order. One of the major problems in detailed studies is the lack of taxonomic effort currently available. Barnard (1958) highlighted this problem for the Gammaridea. He showed that despite the great increases in material available for study, the systematic activity was considerably less than during the 1930s. Although Barnard himself has made massive contributions to amphipod systematics, the problem is still acute, and effort is not commensurate with the volume of specimens being obtained. Many of the major faunules are still very poorly known (witness Barnard (1972, 1974) working on non-domicolous, non-fossorial amphipods from shallow water environments in warm temperate Australia, who discussed 47 genera of which 18 were

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new, and 124 species of which 84 were new). That systematic effort is still a prime requisite in the study of deep sea amphipods is shown by a series of four papers by Barnard (1961, 1962, 1964, 1967). In the four collections dealt with 64%, 63%, 59% and 52% respectively of the species discussed were new to science. The relatively low figure of 52% reflects previous work in the same small area by Barnard himself (1966).

Brook (1974), in discussing the zoogeography of the deep sea, has collated data from many sources which indicate that most invertebrate groups, including amphipods (see Barnard (1962)), contain a high proportion of species which appear to be endemic to single ocean basins. Although future work may well reduce the apparently high endemicity in the deep sea, there is no indication that the descriptive effort within the Gammaridea, and probably most other major invertebrate groups, has reached a level of diminishing returns.

Taxonomy, although a legitimate end in itself, should also serve as a tool for further studies in the ecology, physiology, zoogeography and related disciplines of the organisms concerned. It is in this light that the present paper is presented.

Material and methods

The five epibenthic sledge hauls made in the vicinity of 60°N 20°W produced 267 specimens of *Rhachotropis.* These specimens represented 7·5% of the total amphipod catch.

The epibenthic sledge, designated BN2·4, which was used to obtain these samples, is a modified beam trawl with a mouth area of $2{\cdot}4m^2$. The framework consists of two vertical, oval structures, each equipped with a broad skid to prevent sinking in soft bottoms and connected at the top by two transverse metal bars. The net, which is 6·10m long and with a mouth 2·44m, by 0·91m, is made of 4·5mm mesh. It is lined for 2·44m in front of the canvas cod-end with 1mm netting. The net is laced to the rearmost of the two transverse bars on the framework, clipped to vertical side wires and laced to a solid bottom bar which is connected by weak links to the heel of the skid of each vertical frame. The sides and top of the main framework are lined with 6mm polypropylene mesh to prevent the escape of animals disturbed by the tickler chain. A depth telemetering pinger akin to that discribed by Clarke (1969), but incorporating a mercury switch, was attached to the framework of the net. This device monitored the changes in angle of attack of the sledge which marked arrival on and departure from the bottom. A subsequent modification of this sledge which incorporates photographic and opening/closing capabilities is designated BN 1·5 and has been described by Aldred *et al* (1976).

Catches consisted of animals and a variable, but usually large, volume of sediment. Large and delicate organisms were picked out of the sediment prior to sieving through 2mm and 500μm meshes. The separated fractions were fixed in 5% formalin and transferred to 70% alcohol 48–72 hours later. Some amphipods were picked out during initial shipboard sorting, but most were recovered in the laboratory.

The positions listed in Table 1 are best estimates of the first and last bottom contact for each haul. Positions, depths and lengths of haul have been calculated from satellite navigation fixes and precision echosounder records.

Thoracic limbs are referred to as gnathopods 1–2 and peraeopods 3–7. Lengths have been taken on straightened animals and were measured from the tip of the rostrum to the tip of the telson. Males have been identified by the presence of genital papillae and females by oostogites; all other specimens being regarded as juveniles.

The specific epithets applied to new species are derived from personal names occurring in the rich Icelandic literature of the Viking period.

Systematics

Over 3500 specimens of gammarid amphipod belonging to about 120 species were obtained from the five epibenthic sledge hauls. Although several species, particularly some lysianassids, were probable contaminants from meso- and bathypelagic midwater zones, a preliminary examination suggests that 94% of the species and over 99% of the specimens were benthic in origin. These data suggest that contamination of catches by midwater organisms is of little significance. This observation is supported by the very small catches made during other hauls which were terminated without bcttom contact.

Over 50% of the benthic species appear to be undescribed. This proportion of new species corresponds closely with the levels found in similar collections studied by Barnard (see above).

The bottom sampled by all five hauls consisted of dark grey-brown mud containing small quantities of larger particles together with some pteropod shells (mainly *Diacria trispinosa*).

Table 1 Station List

Station	Date	Position	Gear	Depth	Length of haul (m)
7709 #62	1 May 1971	59°58·8′N 19°58·2′W – 59°58·8′N 19°58·8′W	BN2·4	2714(–0)m	1010
7709 #66	3 May 1971	59°59·4′N 19°53·5′W – 59°58·3′N 19°53·5′W	BN2·4	2712(–0)m	2150
7709 #72	5 May 1971	60°05·7′N 19°43·3′W – 60°06·8′N 19°42·5′W	BN2·4	2663–2649(–0)m	2450
7709 #73	5 May 1971	60°07·5′N 19°32·4′W – 60°06·4′N 19°26·6′W	BN2·4	2646–2636(–0)m	9460
7709 #85	7 May 1971	59°58·6′N 19°53·4′W – 59°58·1′N 19°54·3′W	BN2·4	2708(–0)m	1690

Rhachotropis proxima Chevreux, 1911
(Figs. 1–2)

Rhachotropis proxima Chevreux, 1911: 11–13, fig. 5; 1935: 110–111, pl. 12, fig. 3.—Stephensen, 1944: 15.—Gurjanova, 1955: 184 (in key).—Barnard, 1957: 14.

Rachotropis proxima (err.)—Schellenberg, 1955: 194.—Belloc, 1960: 13.

MATERIAL EXAMINED. Sta. 7709 #62 1♀ 9mm, 4 damaged specimens; Sta. 7709 #66 1 damaged specimen; Sta. 7709 # 72 5♂ 12–14mm, 1 ovig. ♀ 17mm, 7♀ 14–17mm, 1 juv. 8mm, 2 damaged specimens; Sta. 7709 #73 8♂ 10–15mm, 28♀ 8–15mm, 7 juv. 7–9mm; Sta. 7709 #85 2♂ 9–12mm, 7♀ 14–19mm, 2 damaged specimens.

DESCRIPTION. Male, 15mm, from Sta. 7709# 73. *Pleon,* each segment weakly carinate, produced posteriorly into low, acute tooth; segments 1 and 2 with small dorso-lateral teeth on posterior margin. *Epimera,* first rounded ventrally; second produced anterior-ventrally, posteriorly sub-rectangular; third similar in shape to second but with six small teeth at posterior distal angle. *Urosome,* first segment with acute dorsal tooth on posterior margin, lacking lateral carinae.

Head, rostrum long, deep and down-curved, as long as head; eyelobes produced, rounded, eyes not seen; postantennal angle bilobed, weak; epistome just more prominent than upper lip. *Antenna 1,* as long as head, peraeon and first pleon segment combined; first article of penducle rather stout, equal to second and third combined, shorter than rostrum; second and third articles more slender than first, second three times length of third; flagellum more than twice as long as peduncle, basal third somewhat inflated, articles short, bearing many elongate aesthetes medially, distal articles long and slender; accessory flagellum of one article, minute, bearing three setae and a spine apically. *Antenna 2,* as long as head, peraeon and first two pleon segments combined; fifth article of peduncle long and slender, as long as first four peduncle articles combined; flagellum nearly twice as long as peduncle, consisting of 44 slender articles. *Upper lip* entire, truncate distally. *Mandible,* incisor process well

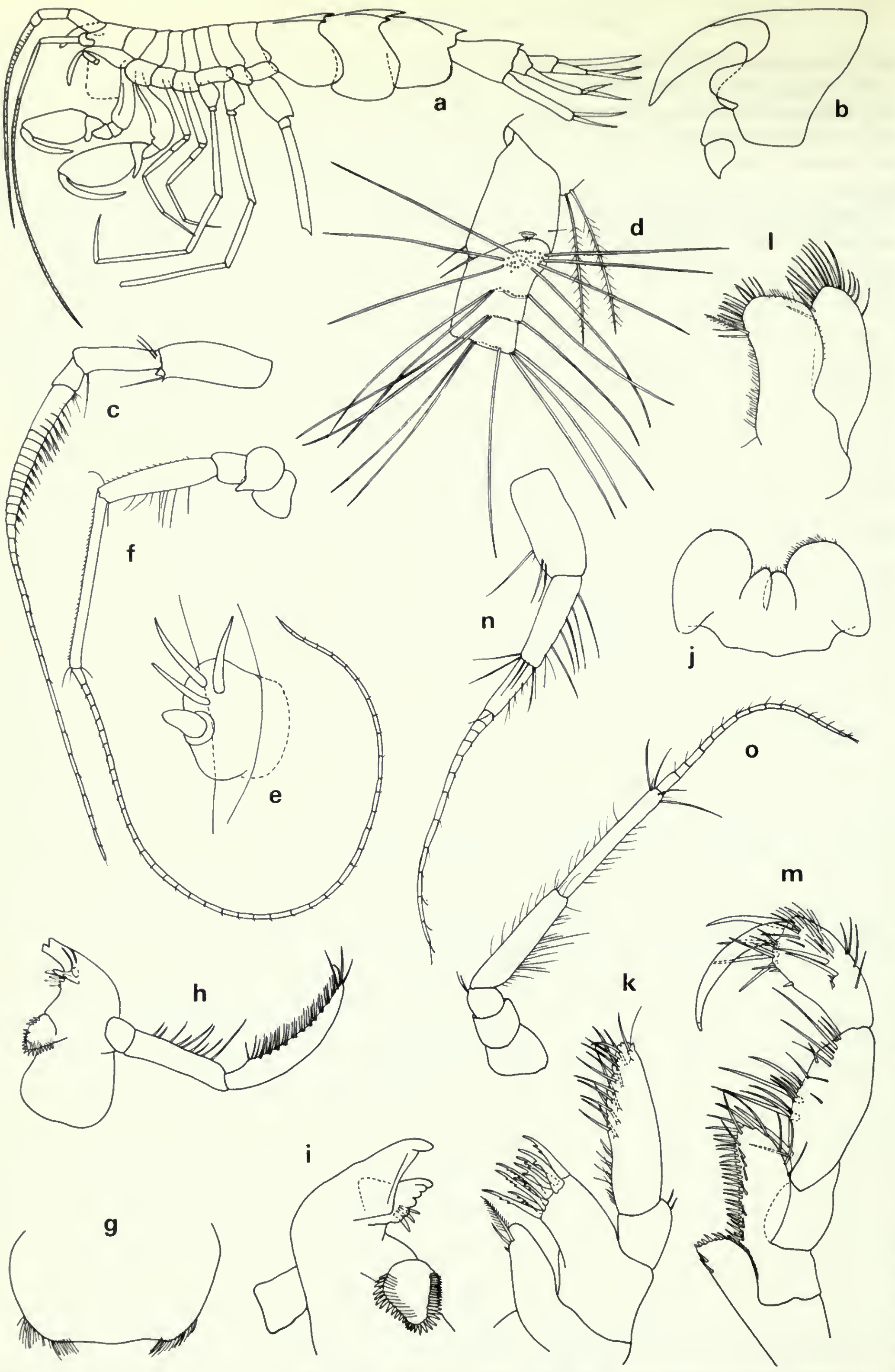

Fig. 1 *Rhachotropis proxima.* Male, 15mm. (a) habitus; (b) head; (c) antenna 1; (d) antenna 1, detail; (e) accessory flagellum; (f) antenna 2; (g) upper lip; (h) right mandible; (i) left mandible, detail; (j) lower lip; (k–l) maxillae 1 & 2; (m) maxilliped. Female, 15mm. (n–o) antennae 1 & 2.

developed with a single tooth and long chitinized cutting edge, lacina mobilis of right mandible with three teeth, of left mandible broader and with six teeth; molar well developed, ridged and bearing marginal teeth; palp longer than body of mandible, third article falciform, densely setose along most of anterior margin, *Lower lip,* inner lobes well developed. *Maxilla 1,* inner plate rather narrow with two subapical setae; outer plate bearing nine slender dentate spines; palp article 2 with serrate, very oblique apex, armed with anterior and posterior rows of setae. *Maxilla 2,* inner plate rather broad, apex rounded, truncate, medial angle armed with stiff setae; outer plate narrower than inner, apically rounded and armed with stiff setae. *Maxilliped,* inner plate small; outer plate narrow with many spine teeth medially; palp strong, second article longest, second and third articles armed with setae and long stout spines, dactyl as long as third article, strongly curved.

Gnathopod 1, coxa strongly produced anteriorly, nearly three times as long as high; basal expanded distally, carpus short, lobed posteriorly; propod oval, palm long, armed with setae; dactyl slender, as long as palm. *Gnathopod 2,* coxa pentagonal; basal expanded distally, armed with group of stout setae at anterior-distal corner; carpus short, with long, slender, heavily spined lobe posteriorly, lobe extending as far as palmar angle of propod; propod oval, rather longer than that of gnathopod 1; dactyl slender, as long as palm. *Peraeopod 3,* coxa small, articles slender; basal as long as articles 3 to 5 combined; carpus nearly twice as long as article 4, subequal in length to propod and to dactyl. *Peraeopod 4,* coxa longer than high, excavate posteriorly, distal articles as in peraeopod 3. *Peraeopod 5,* coxa weakly bilobed, posterior lobe stronger, distally rectangular; basal short, expanded distally; merus elongate, slender; carpus shorter and more slender than merus; propod very long and slender, length more than 20 times width; dactyl very slender, slightly curved, about 40% of length of propod. *Peraeopod 6,* coxa with posterior lobe stronger, rectangular at posterior-distal angle; distal articles similar to those of peraeopod 5. *Peraeopod 7,* coxa just acute posterior-distally; basal nearly twice as long as that of peraeopod 6, posterior distal angle acute; fourth article twice as long as basal, slightly produced posterior-distally; carpus more slender than merus and 20% longer; propod elongate and extremely slender, length 25% greater than that of carpus, maximum width less than 3% of length; dactyl straight, very slender, 25% length of propod.

Uropod 1, inner ramus just longer than outer, shorter than peduncle. *Uropod 2,* extends back to apex of uropod 1; inner ramus just shorter than peduncle, with four small spines on medial margin, outer ramus unarmed, 75% as long as inner ramus. *Uropod 3,* rami lanceolate, subequal, margins minutely pectinate, twice as long as peduncle, inner ramus armed on medial margin, outer on both margins. *Telson* as long as uropod 3, broad, sides parallel, tapering distally, cleft 12% of length, armed dorsally with minute spines.

Female, 15mm, from Sta. 7709 #73. Females attain a larger size than males, reaching 18mm, but differ morphologically only in the broader peraeon and shorter antennae. *Antenna 1,* peduncle and flagellum subequal in length; peduncle article 1 stouter and just longer than article 2, article 3 60% length of article 2; flagellum of 12 articles. *Antenna 2,* peduncle article 5 longer and more slender than article 4; flagellum shorter than peduncle articles 4 and 5 combined, of 15 articles.

REMARKS. Barnard (1957) omitted *R. proxima* from his key to the genus on the grounds of uncertainty concerning the dorsal armature of this species. The present material, which agrees precisely with Chevreux's illustrations, reveals an error in the original description (Chevreux, 1911:11). The reference to the dorsal armature of the mesosome in fact applies to the metasome. No species of *Rhachotropis* has yet been described in which peraeon and urosome are carinate and dentate, but the pleon unarmed.

R. proxima belongs to the group of species characterized by a strongly produced coxa 1, peraeonite 7 without teeth, pleonites 1–3 with three, three and one tooth respectively and urosomite 1 dentate.

Two species, *R. kergueleni* Stebbing, 1888 and *R. hunteri* Nicholls, 1938, agree with these basic characters of *R. proxima. R. proxima* is closely related to *R. kergueleni,* but the

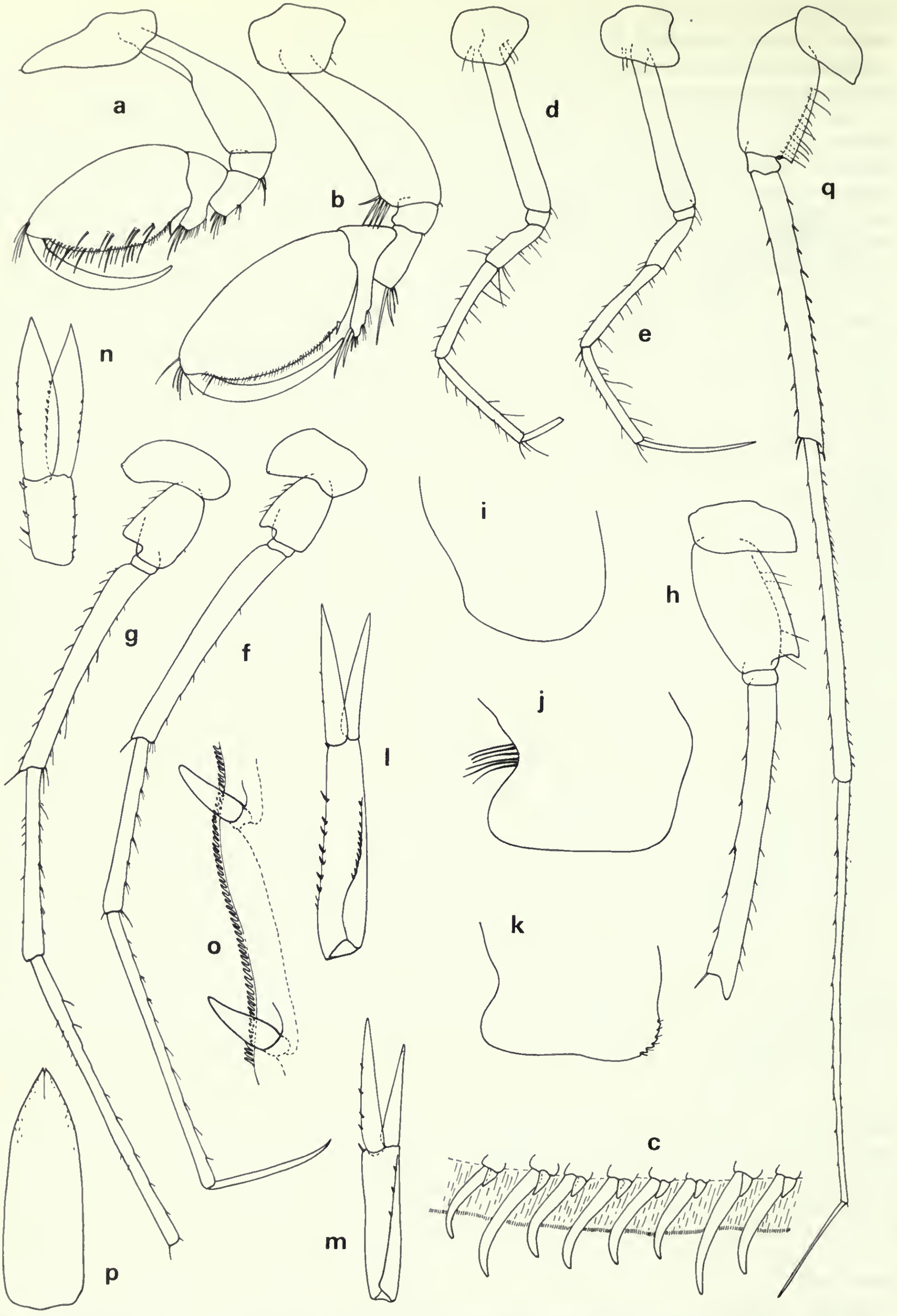

Fig. 2 *Rhachotropis proxima.* Male, 15mm. (a–b) gnathopods 1 & 2; (c) gnathopod 2, detail of palm; (d–h) peraeopods 3–7; (i–k) epimera 1–3; (l–n) uropods 1–3; (o) uropod 3, margin of outer ramus; (p) telson. Male, 14mm. (q) peraeopod 7.

southern hemisphere species has a large tooth on urosomite 1, broadly rounded and strongly serrate epimeron 3, a less deeply cleft telson with divergent apices, and basal articles of peraeopods 5–7 with serrate posterior margins. The distinction between those two species is obscured somewhat by specimens doubtfully assigned to *R. kergueleni* by Stephensen (1944a). In the dehiscent apices of the telson and broadly rounded, strongly serrate epimeron 3, the 'Ingolf' material from the Davis Strait agrees with *R. kergueleni* while the weakly serrate basal articles of peraeopods 5–7 are closer to *R. proxima*. The degree of variation of these characters in the present specimens is minimal so until the status of Stephensen's specimens and the type material of *R. kergueleni* can be clarified, it seems best to exclude both these entities and maintain *R. proxima* as distinct.

Two new species described later in this paper are related to *R. proxima*. One possesses the same basic characters as *R. proxima* and the other differs in the condition of coxa 1. The diagnostic characters are discussed on p. 53 and p. 57 respectively.

A number of other species are also related to *R. proxima*. *R. levantis* Barnard, 1961 and *R. anoculata* Barnard, 1962 both lack teeth on urosomite 1, have telsons cleft more than 30% of their length, and bear calceoli on the antennae. In addition the shape of the basal articles of peraeopods 5–7 is markedly different in *R. levantis* and *R. proxima*. The dorsal posterior margin of pleonite 3 is prominent but not dentate in *R. anoculata*, thus contrasting with *R. proxima* in which this segment bears a distinct tooth. *R. leucophthalma* Sars, 1893, *R. sibogae* Pirlot, 1934, *R. integricauda* Carausu, 1949, *R. cervus* Barnard, 1957 and *R. flemmingi* Dahl, 1959 all differ from *R. proxima* in possessing dorso-lateral teeth on pleonite 3 in addition to the median tooth. *R. integricauda* is unique in the genus in having an uncleft telson. *R. leucophthalma* and *R. cervus* can also be separated from *R. proxima* by the telson which is cleft 50% and 30% of its length respectively as opposed to 14–17%. *R. sibogae* is further distinguished from *R. proxima* by the broadly rounded coxa 1, the form of epimeron 3 and the divergent apices of the telson. Peraeopod 7 of *R. flemmingi* has an extremely long propod, which is as long as the fourth and fifth articles combined, and a dactyl half the length of the propod. These proportions are significantly different in *R. proxima* as is the condition of epimeron 3. *R. antarctica* Barnard, 1932 and *R. clemens* Barnard, 1967 are separable from *R. proxima* in that they lack teeth on pleonite 3. *R. antarctica* has eyes, dorso-lateral keels on pleonite 1 and on urosomite 1, and a broadly expanded basal article of peraeopod 7, features not present in *R. proxima*. A short rostrum, weakly produced coxa 1, slender basal articles of peraeopods 5 and 6 and a large tooth on urosomite 1 are additional characters separating *R. clemens* from the present species. *R. platycera* Barnard, 1931 is much smaller than *R. proxima*, adults reaching only 4·5mm as opposed to 12–20mm, and has calceolate antennae, eyes, a dorsal tooth on peraeonite 7 and a deeply cleft telson.

Rhachotropis thordisae sp. nov.

(Figs. 3–4)

MATERIAL EXAMINED. Sta. 7709#62 2♂ 10mm, 6♀ 7–11mm, 1 juv. 6mm, 1 damaged specimen; Sta. 7709#72 12♂ 5–10mm, 5 ovig. ♀ 10–11mm, 15♀ 7–12mm, 9 damaged specimens; Sta. 7709#73 12♂ 5–10mm, 1 ovig. ♀ 10mm, 20♀ 7–11mm, 5 juv. 4–6mm, 1 intersex 9mm, 2 damaged specimens; Sta. 7709#85 1♂ 9mm, 5♀ 7–11mm, HOLOTYPE ♂ BM(NH) reg. no. 1978: 218 [carcase and 4 microscope preparations], ALLOTYPE 1978: 219, PARATYPES 1978: 220.

Material from Sta. 7709#85 has been deposited in the collections of the Zoology Department of the British Museum (Natural History), and specimens from the remaining three stations are held at the Institute of Oceanographic Sciences.

ETYMOLOGY. Thordis Thorbjornsdottir, sister of Gisli.

DESCRIPTION. Holotype, male, 9mm. *Pleon*, each segment produced posteriorly into a dorsal tooth; segment 1 with procumbent lateral teeth; segment 2 carinate nearly square in transverse section due to well-developed, dorso-lateral carinae each ending in prominent tooth;

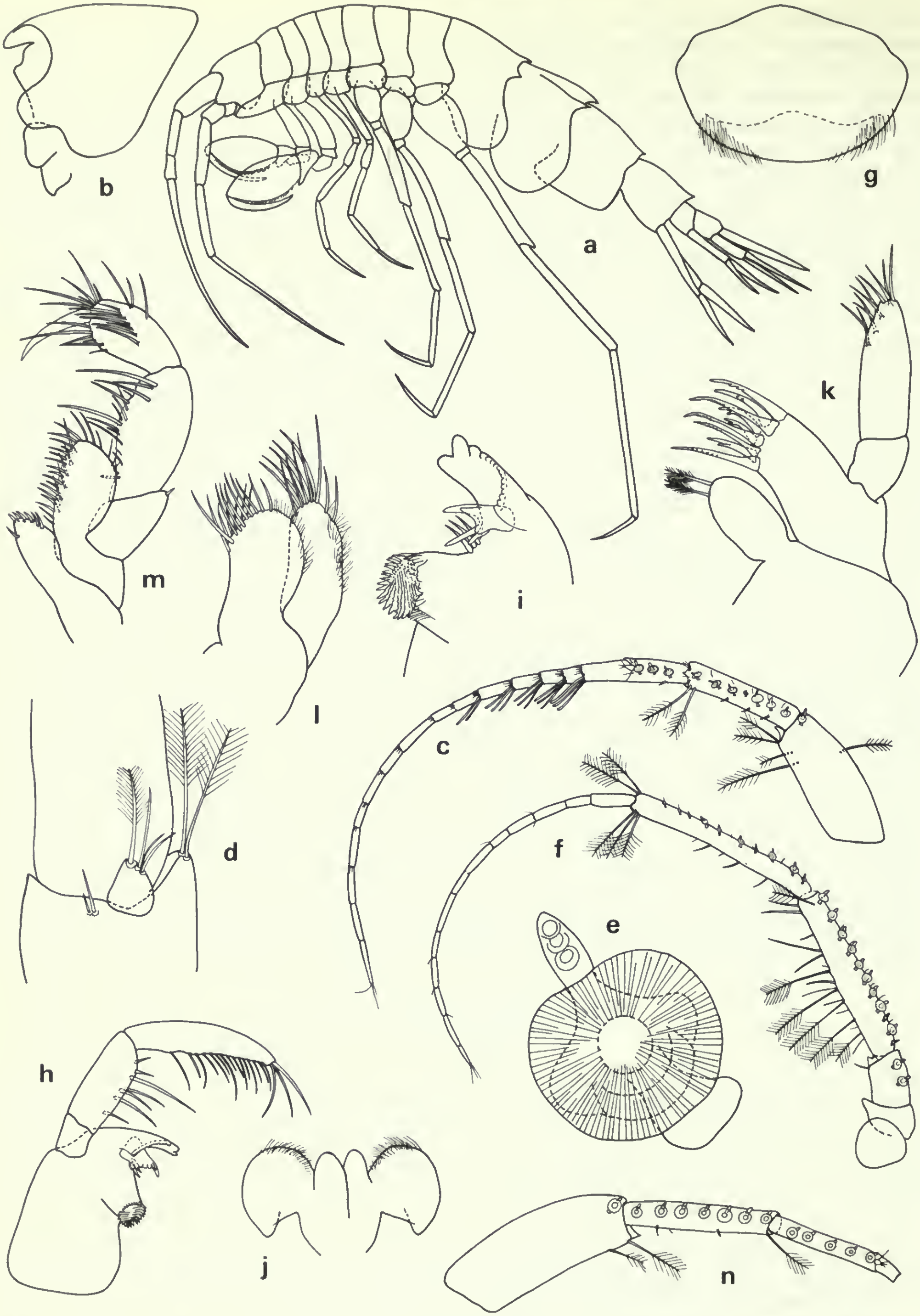

Fig. 3 *Rhachotropis thordisae* sp. nov. Holotype, male, 9mm. (a) habitus; (b) head; (c) antenna 1; (d) accessory flagellum; (e) calceolus from peduncle of antenna 1; (f) antenna 2; (g) upper lip; (h) left mandible; (i) right mandible, detail; (j) lower lip; (k–l) maxillae 1 & 2; (m) maxilliped. Allotype, female, 11mm. (n) antenna 1.

segment 3 carinate, mid-dorsal tooth small. *Epimera,* first rounded ventrally; second deep, rounded, somewhat flattened posterior-ventrally, with small submarginal spines ventrally and fine setae posteriorly; third, ventral margin straight, posterior margin gently convex, serrate. *Uromsome,* first segment weakly carinate carina ending in acute tooth.

Head, rostrum slightly downcurved, short, about one-fifth length of first peduncle article of antenna 1; eyelobes produced, rounded, apically somewhat obtuse, eyes not seen; post-antennal lobe weak; epistome produced in front of upper lip. *Antenna 1,* as long as head, peraeon and first pleon segment combined; first article of peduncle rather stout with short, acute tooth ventro-distally, just shorter than articles 2 and 3 combined, bearing single calceolus distally on medial surface; article 2 about four-fifths length of article 1 with seven calceoli medially; article 3 half length of article 2, three calceoli on medial surface; flagellum half as long again as peduncle, of 15 articles, the first five slightly expanded, bearing elongate aesthetes; accessory flagellum short, triangular. *Antenna 2,* just longer than antenna 1; article 3 short, toothed posterior-distally; articles 4 and 5 subequal in length; articles 3, 4 and 5 bearing two, eleven and eleven calceoli respectively along length of anterior-medial surfaces; flagellum a little shorter than peduncle, of 14 articles. *Upper lip* broadly rounded, setose disto-laterally. *Mandible,* incisor process, strong, with two or three teeth and long chitinized cutting edge; lacina mobilis of left mandible with curved multi-dentate cutting edge, of right mandible with five acute teeth; spine row of three pectinate spines; molar strong, triturating surface ridged and with strong marginal teeth; palp rather stout, longer than body of mandible; article 2 armed with stout setae; article 3 as long as articles 1 and 2 combined, setose along distal three-quarters of posterior margin. *Lower lip,* rather broad, inner lobes prominent, outer lobes densely setose distally. *Maxilla 1,* inner plate oval, bearing two plumose setae distally; outer plate with nine long, very slender dentate spines; palp article two with obliquely truncate apex bearing two rows of marginal and submarginal setae. *Maxilla 2,* small, inner plate broadly rounded with stiff setae medio-apically; outer plate narrower than inner, apex armed with stiff setae. *Maxilliped,* inner plate short with stout spines distally; outer plate armed with stout spines along medial margin; palp well developed, second article longest; dactyl rather slender, weakly curved, as long as third article.

Gnathopod 1, coxa with anterior-ventral angle strongly produced, anterior and ventral margins more than twice as long as posterior margin, posterior-distal angle with small tooth; basal somewhat expanded distally; carpus short, posterior lobe well developed, spinose; propod oval, nearly four times as long as carpus, palm gently convex, armed with graded ranks of pectinate setae; dactyl slender, curved, as long as palm. *Gnathopod 2,* coxa pentagonal, anterior-distal angle more prominent than posterior angle which bears small tooth; carpus strongly produced posteriorly, lobe bearing stout spines and setae; propod a little longer that that of gnathopod 1 but otherwise similar. *Peraeopod 3,* coxa small, trapezoidal, posterior-distal angle with small tooth; article 4 just more than half length of article 5; articles 5–7 subequal in length; dactyl very slender. *Peraeopod 4,* coxa small, height and width subequal, posterior distal angle not produced, posterior margin barely concave; articles 2–7 as in peraeopod 3. *Peraeopod 5,* coxa shallow bilobed, lobes subequal; basal expanded posteriorly, width three-fifths of length, posterior margin evenly rounded, serrate; merus and propod subequal; carpus just longer than merus, length twice that of basal, anterior margin bearing about 20 short spines in addition to longer spines and setae; dactyl very slender, distally curved, length three-fifths of carpus. *Peraeopod 6* a little longer than peraeopod 5; coxa bilobed, posterior lobe stronger and bearing small tooth posteriorly; articles 4–6 subequal in length, twice as long as basal; carpus armature similar to that of peraeopod 5; dactyl very slender, curved distally just more than half as long as propod. *Peraepod 7,* longer than peraeopod 6; coxa small, bearing three small teeth posterior-distally; basal oval, posterior margin serrate; carpus longer than merus, twice as long as basal; propod very slender, one-fifth longer than carpus; dactyl slender, curved distally, one-third length of propod.

Uropod 1, rami shorter than peduncle, narrowly lanceolate, margins finely pectinate.

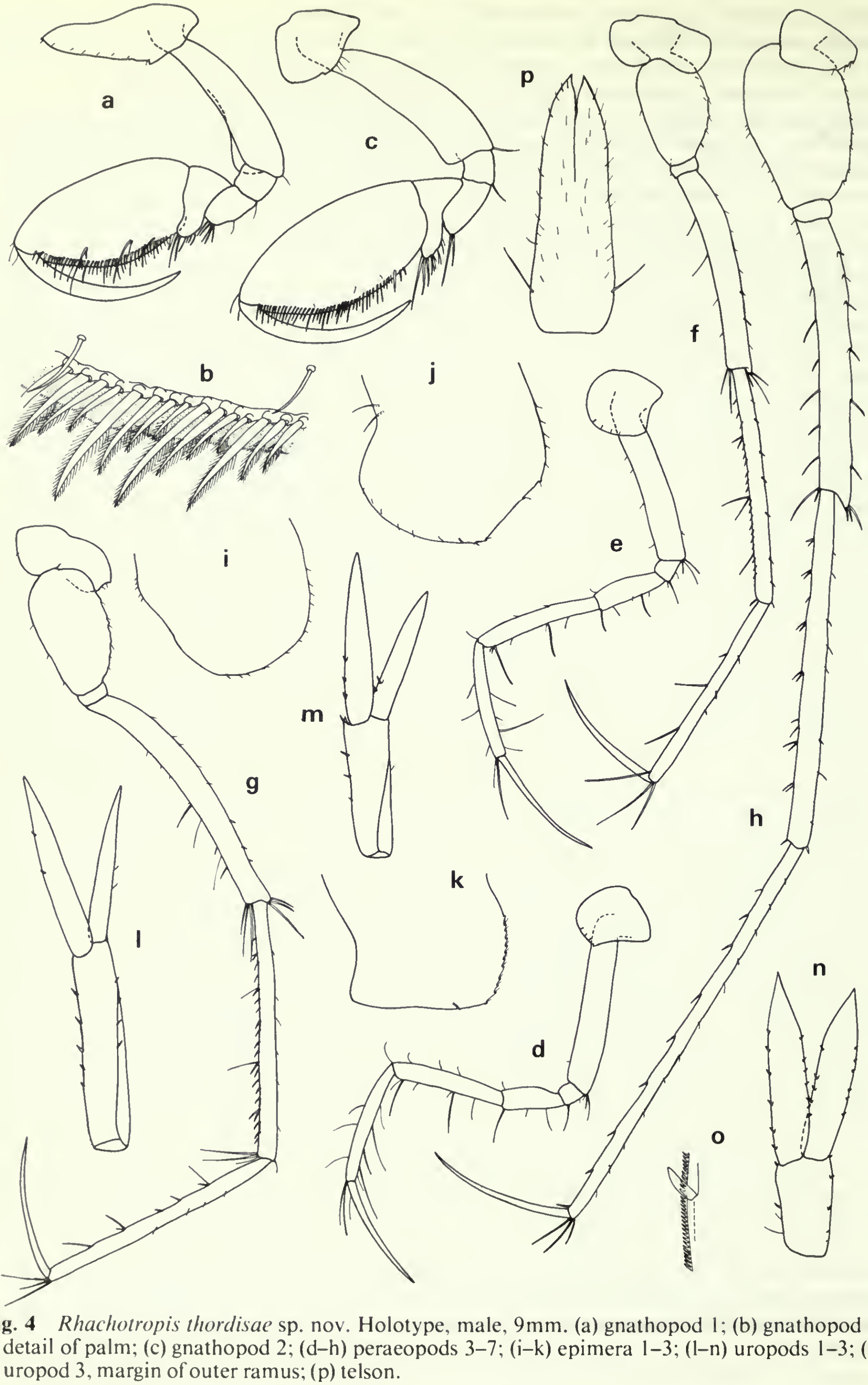

Fig. 4 *Rhachotropis thordisae* sp. nov. Holotype, male, 9mm. (a) gnathopod 1; (b) gnathopod 1, detail of palm; (c) gnathopod 2; (d–h) peraeopods 3–7; (i–k) epimera 1–3; (l–n) uropods 1–3; (o) uropod 3, margin of outer ramus; (p) telson.

Uropod 2, extends back only as far as apex of inner ramus of uropod 1, outer ramus and peduncle subequal in length, inner ramus one-fifth longer, margins of both rami finely pectinate. *Uropod 3,* rami broadly lanceolate, much longer than peduncle, all margins of rami pectinate and bearing short spines. *Telson* more than three times so long as wide, cleft 43% of length, margins subparallel over most of length tapering distally, apices acute, a little divergent.

Allotype, female, 11mm. Differs from holotype mainly in structure of antenna 1. *Antenna 1,* penduncle article 1 rather stout, bearing small tooth latero-distally and single discoidal calceolus medio-distally; article 2 more slender, four-fifths length of article 1, with 7 calceoli on medial surface; article 3 three-quarters length of article 2, bearing five calceoli medially; basal articles of flagellum not expanded, lacking aesthetes.

REMARKS. *R. thordisae* belongs to the group of species characterized by an edentate seventh peraeon segment, pleonites with three, three and one teeth respectively, urosomite 1 dentate and coxa 1 strongly produced.

Three other species also possess these characters. *R. kergueleni* can be separated from *R. thordisae* by the long rostrum, posteriorly serrate and posterior-distally produced basal articles of peraeopods 5–7, and shallowly cleft telson of the former species. *R. thordisae* and *R. proxima* are distinguishable by the short rostrum, calceolate antennae and deeply cleft, telson of the former. A further means of separation is the shape of the basal articles of peraeopods 5–7; posterior-distally rounded in the present species and acutely produced in *R. proxima. R. hunteri* differs from *R. thordisae* in possessing a long rostrum, and a very short outer ramus on uropod 2. *R. thordisae* also has a rather more deeply cleft telson (40% of length) than does *R. hunteri.*

R. leucophthalma, R. sibogae, R. integricauda, R. cervus and *R. flemmingi* conform to the basic diagnosis of *R. thordisae* except that all possess dorso-lateral teeth on pleonite 3. Additional characters separating these species from *R. thordisae* are the tricarinate pleonite 1 and urosomite 1, and the form of the basal article of peraeopod 7 of *R. leucophthalma*; the long rostrum, broadly rounded anterior-distal apex of coxa 1, posterior-distally produced basal article of peraeopod 7, and shallowly cleft telson of *R. sibogae*; the dorso-lateral carinae on pleonites 1 and 3, and the form of coxae 1, 4 and 6 and of epimeron 3 of *R. cervus*; and the posterior-distally produced basos and elongate propod and dactyl of peraeopod 7 and the less deeply cleft telson of *R. flemmingi. R. antarctica* and *R. clemens* both differ from *R. thordisae* in lacking teeth on pleonite 3. In addition *R. antarctica* has pleonites 1 and 3 and urosomite 1 tricarinate, and is oculate, while *R. clemens* has a relatively long rostrum, slender basal articles of peraeopods 5–6 and a shallowly cleft telson. *R. anoculata* lacks teeth on pleonite 3 and urosomite 1. *R. platycera* can be distinguished from *R. thordisae* by the possession of eyes and a tooth on peraeonite 7 in the former species. *R. levantis* has dorso-lateral carinae on pleonite 3 and urosomite 1 but lacks a tooth on the latter segment, and is further separated from *R. thordisae* by the long rostrum, and by the form of the basal articles of peraeopods 5–7 and epimeron 3.

Rhachotropis thorkelli sp. nov.
(Figs. 5–6)

MATERIAL EXAMINED. 1. Sta. 7709#73 4♂ 6–9mm, 1♀ 7mm, HOLOTYPE ♂ BM(NH) reg. no. 1978: 221 [carcase and four microscope preparations], ALLOTYPE 1978: 222, PARATYPE 1978: 223. Two paratypes have been retained at the Institute of Oceanographic Sciences.

ETYMOLOGY. Thorkell Thorbjornsson, elder brother of Gisli.

DESCRIPTION. Holotype, male, 9mm. *Pleon,* all segments weakly carinate dorsally; pleonites 1 and 2 each drawn out into a posteriorly directed dorsal tooth and a pair of large decumbent dorso-lateral teeth; pleonite 3, dorsal tooth prominent but not posteriorly produced. *Epimera,* first rounded ventrally, somewhat produced posteriorly; second, broadly rounded at posterior-distal angle; third, broadly rounded posterior-distal angle armed with three small setae, posterior margin irregularly convex. *Urosome,* dorsally carinate, carina ending in acute tooth.

Head, rostrum deep, rather short, projecting beyond eyelobes; epistome rounded, sharply separated from medial crest on anterior of head. *Antenna 1,* as long as head, peraeon and first pleonite combined: first article of peduncle stout, just longer than more slender second article; third article about one-third as long as first; flagellum nearly half as long again as peduncle, basal part somewhat inflated, articles short and bearing many elongate aesthetes, distal articles long and slender; accessory flagellum minute. *Antenna 2,* nearly as long as body; peduncle article 5 slender, longer than articles 1–4 combined; flagellum nearly half as long again as peduncle, of 34 slender articles. *Upper lip,* broadly convex, setose. *Left mandible,* cutting edge entire with single distal tooth, lacina mobilis stout and with five teeth, two spines in spine row, molar prominent, ridged and toothed; palp much longer than body of mandible, article 3 slightly curved, densely setose along distal four-fifths of anterior margin, longer than articles 1 and 2 combined. *Right mandible,* incisor with long cutting edge armed with three teeth, lacina mobilis rather slender, with four teeth, spine row of three spines. *Lower lip,* inner lobes prominent, outer lobes densely setose. *Maxilla 1,* inner plate distally rounded, bearing subterminal plumose seta; outer plate with nine slender dentate or pectinate spines; palp rather slender, armed with setules and spines. *Maxilla 2,* inner plate broadly rounded, apex with fine setules, medial-distal angle armed with stout setae; outer plate more slender, rounded apex armed with spines and stout setae. *Maxilliped,* inner plate transversely truncate, bearing six stout spine teeth distally; outer plate broadly expanded, lateral-distal margin with long curved spines, inner margin with many slender spine teeth; palp long, well developed, article 2 the longest, articles 2 and 3 bearing many stout setae on and near medial margins, dactyl slender, rather shorter than article 3.

Gnathopod 1, coxa acutely produced, anterior and proximal margins subequal; basal expanded distally, channelled, with group of stout setae anteriorly; carpus short, posterior lobe well developed, bearing groups of long setae, and a stout spine apically; propod twice as long as wide, palm convex, armed with short, closely spaced spines; dactyl curved, as long as palm. *Gnathopod 2,* coxa broadly rounded, somewhat produced anteriorly; basal channelled anteriorly, distally expanded; carpus short, posterior lobe slender, strongly developed, reaching nearly to palmar spines; propod oval, rather longer than that of gnathopod 1, palm evenly convex, armed with short closely set spines; dactyl as long as palm. *Peraeopod 3,* coxa short, broadly rounded and somewhat produced anteriorly; basal slender; merus stout, short, two-fifths length of carpus; carpus slender subequal in length to basal and dactyl; propod about three-quarters length of carpus. *Peraeopod 4,* coxa somewhat produced and broadly rounded anteriorly, shallowly excavate posteriorly, posterior-distal angle rounded, obtuse; distal articles similar to those of peraeopod 3. *Peraeopod 5,* coxa bilobed, lobes subequal; basal somewhat expanded posteriorly, subrectangular; merus curved, more than twice as long as basal; distal articles lost. *Peraeopod 6,* coxa bilobed, anterior lobe short, subacute, posterior lobe strong, broadly rounded; basal slightly expanded, anterior and posterior margins parallel; merus curved, more than twice as long as basal, distal articles lost. *Peraeopod 7,* coxa suboval, produced posteriorly; basal expanded, margins parallel; merus straight, half as long again as basal; distal articles lost.

Uropod 1, inner ramus unarmed, one-tenth longer than outer ramus, three-quarters length of peduncle. *Uropod 2,* rami lanceolate, unarmed, inner equal in length to peduncle, outer three-quarters length of inner. *Uropod 3,* peduncle with seven short spines on inner margin; rami lanceolate, inner one-fifth and outer one-eighth longer than peduncle. *Telson,* long, linguiform, cleft 7% of length, apices acute, divergent.

Allotype, female, 7mm. *Pleon,* not carinate, pleonite 3 dorsal tooth posteriorly produced. *Antenna 1,* peduncle articles 1 and 2 equal in length and about twice as long as article 3; flagellum of seven slender articles, a little shorter than peduncle. *Antenna 2,* about one-fifth longer than antenna 1; peduncle articles 4 and 5 slender, fifth article one-sixth longer than fourth; flagellum three-fifths length of peduncle, consisting of ten slender articles.

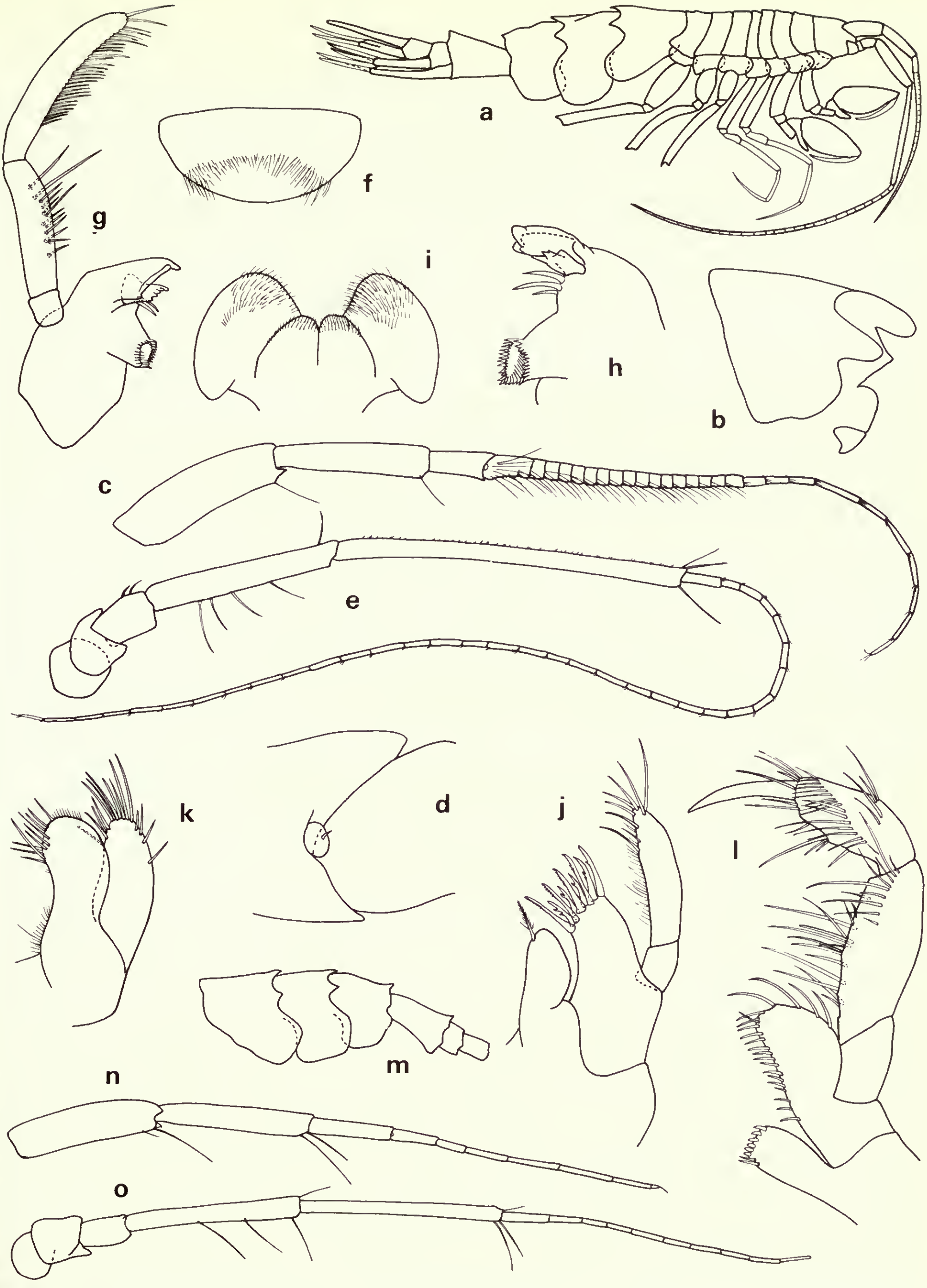

Fig. 5 *Rhachotropis thorkelli* sp. nov. Holotype, male, 9mm. (a) habitus; (b) head; (c) antenna 1; (d) accessory flagellum; (e) antenna 2; (f) upper lip; (g) left mandible; (h) right mandible, detail; (i) lower lip; (j–k) maxillae 1 & 2; (l) maxilliped. Allotype, female, 7mm. (m) pleon and urosome; (n–o) antennae 1 & 2.

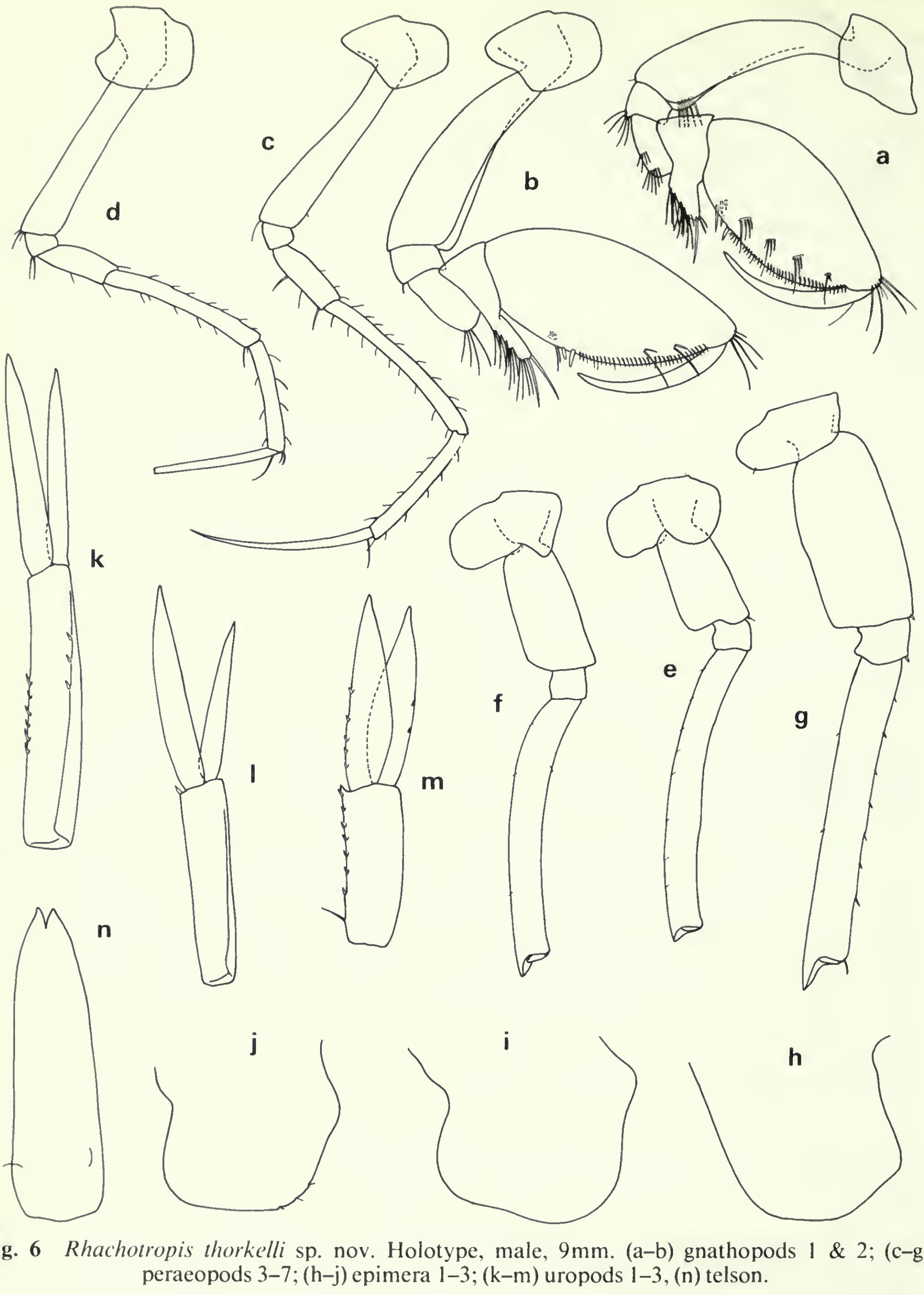
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Fig. 6 *Rhachotropis thorkelli* sp. nov. Holotype, male, 9mm. (a–b) gnathopods 1 & 2; (c–g) peraeopods 3–7; (h–j) epimera 1–3; (k–m) uropods 1–3, (n) telson.

REMARKS. *R. thorkelli* belongs among those species which lack teeth on peraeonite 7, have three, three, one and one teeth on pleonites 1–3 and urosomite 1, and a weakly produced first coxa.

A weakly produced coxa 1 is a minority trend within *Rhachotropis*. Although a number of species have a pattern of dorsal armature agreeing with that of *R. thorkelli*, most also have coxa 1 strongly produced. *R. kergueleni, R. proxima, R. hunteri* and *R. thordisae* fall into this category. Further means of separating *R. thorkelli* from these species are the longer rostrum and strongly serrate basal articles of peraeopods 5–7 and epimeron 3 of *R. kergueleni;* the very long rostrum posteriorly produced basal articles of peraeopod 5–6 and form of epimeron 3 of *R. proxima;* the longer rostrum, short outer ramus of uropod 2 and more deeply cleft telson of *R. hunteri;* and the tricarinate pleonite 2, calceoliferous antennae, oval basal articles of peraeopods 5–7, serrate epimeron 3 and deeply cleft telson of *R. thordisae.* The condition of coxa 1 in *R. integricanda* has not been described, but this species can be separated from *R. thorkelli* by the uncleft telson and tridentate pleonite 3. Differences between the present species and a further new species with weakly produced coxa 1 are discussed on p. 61.

Rhachotropis gislii sp. nov.
(Figs. 7–8)

MATERIAL EXAMINED. Sta. 7709 # 62 1♂ 12mm, 2 damaged specimens; Sta. 7709 # 66 2♀ 11–13mm, 1 juv. 7mm, 1 damaged specimen; Sta. 7709 # 72 4♂ 9–12mm, 1 ovig. ♀ 12mm, 9♀ 8–13mm, 4 juv. 5–7mm; Sta. 7709 # 73 5♂ 10–12mm, 1 ovig. ♀ 13mm, 16♀ 8–14mm, 4 juv. 5–6mm, 1 damaged specimen, HOLOTYPE ♀ BM(NH) reg. no. 1978: 224 [carcase and 4 microscope preparations], ALLOTYPE 1978: 225, 3 PARATYPES 1978: 228, 13mm figured ♀ 1978: 226. Sta. 7709 # 85 2♂ 11–12mm, 3♀ 8–12mm, 3 juv. 7mm. Figured ♂, 11mm, BM(NH) reg. no. 1978: 227.

All registered type and figured material has been deposited in the Zoology Department of the British Museum (Natural History); other material has been retained at the Institute of Oceanographic Sciences.

ETYMOLOGY. Gisli, son of Thorbjorn Thorkellsson, whey-Thorbjorn.

DESCRIPTION. Holotype, female, 14mm. *Pleon,* each segment produced into posterior-dorsal tooth; pleonite 1, tooth acute, nearly vertical, strong backwardly projecting lateral teeth; pleonite 2, dorsal tooth long, slender, lateral carinae ending in backwardly projecting teeth; pleonite 3, dorsal tooth weakly carinate anteriorly, backwardly projecting. *Epimera,* first rounded; second, distally rounded, posterior margin nearly straight, finely serrate posteriorly on distal margin; third subrectangular, serrate distally and posteriorly. *Urosome,* first segment without tooth or lateral carinae.

Head, humped dorsally near posterior margin, rostrum rather short, concave transversely near base; eyelobes projecting somewhat ventrally, as long as rostrum, distally rounded; post-antennal lobe broadly rounded, weak; epistome, broadly rounded, just projecting beyond upper lip. *Antenna 1,* article 1 rather stout, shorter than head, subequal to more slender second article; article 3 one-third length of article 2; flagellum not much longer than peduncle, of 15 articles; accessory flagellum very small, articulated, bearing three short subterminal spines. *Antenna 2,* a little longer than antenna 1, peduncle articles 4 and 5 subequal; flagellum just shorter than peduncle, of 19 articles. *Upper lip,* broadly rounded with subapical corona of setae. *Mandibles,* incisor process strongly chitinized with one or two blunt teeth ventrally; lacina mobilis of left mandible with five blunt teeth, of right mandible with three digitate teeth; spine row with three or four stout spines; molar process columnar with prominent teeth and ridges on triturating surface; palp shorter than body of mandible, third article, slender, just shorter than second, bearing eight setae disto-laterally. *Lower lip,* inner lobes prominent, outer lobes densely setose. *Maxilla 1,* inner plate distally truncate, two plumose setae at medio-distal angle; outer plate with nine slender pectinate or dentate

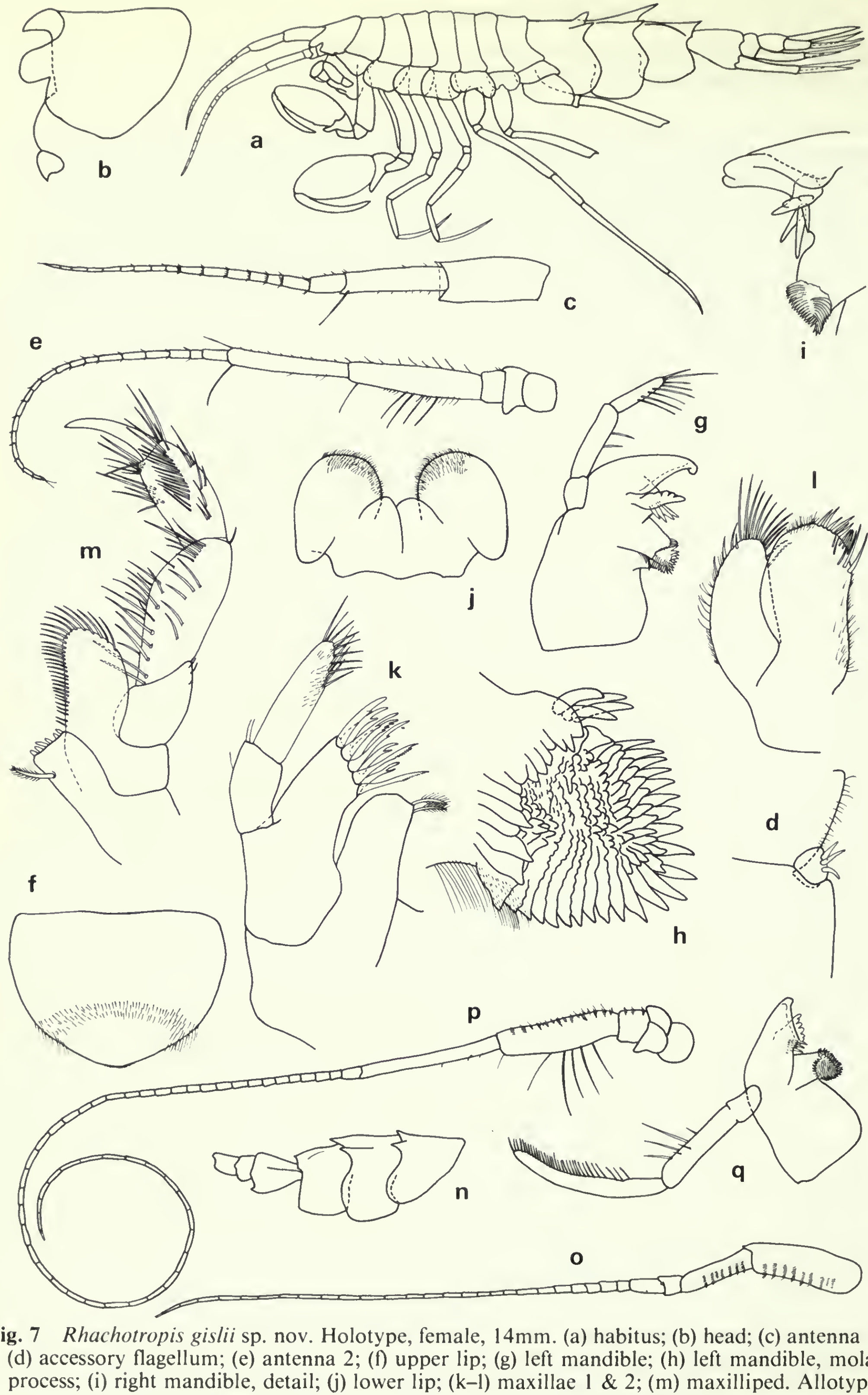

Fig. 7 *Rhachotropis gislii* sp. nov. Holotype, female, 14mm. (a) habitus; (b) head; (c) antenna 1; (d) accessory flagellum; (e) antenna 2; (f) upper lip; (g) left mandible; (h) left mandible, molar process; (i) right mandible, detail; (j) lower lip; (k–l) maxillae 1 & 2; (m) maxilliped. Allotype, male, 12mm. (n) pleon and urosome; (o–p) antennae 1 & 2; (q) left mandible.

spine teeth distally; second palp article slender, apically rounded, bearing spines distally. *Maxilla 2,* short, inner plate as long as outer, rounded, short spines clustered medio-distally; outer plate more slender than inner with three stout spines disto-laterally and series of spine setae on rounded apex. *Maxilliped,* inner plate distally truncate, bearing six short spine teeth; outer plate extending just beyond apex of first article of palp, rather slender, armed medially and distally with graded series of closely set spines; palp well developed, second article the longest, third article armed with many stout setae, dactyl strong.

Gnathopod 1, coxa weakly produced, anterior-distal angle acute; basal anteriorly channelled, with short spines along the length of anterior margin; carpus short, posterior lobe well developed, spinous; propod broadly oval, palm convex, four-fifths length of posterior margin; dactyl curved, as long as palm. *Gnathopod 2,* coxa broadly rounded anteriorly, somewhat produced; basal similar to but a little longer that that of gnathopod 1, bearing fine spines anteriorly; posterior lobe of carpus elongate, densely spinose on medio-posterior surface; propod of same form as that of gnathopod 1 but a little larger, palmar margin armed with ranked spines and pectinate setae; dactyl as long as palm. *Peraeopod 3,* coxa produced anteriorly, rectangular; basal long, slender with comb-like group of spines at posterior-distal angle; articles 4–7 lost. *Peraeopod 4,* coxa longer than deep, pentagonal, distal margin, just concave, emarginate posteriorly, posterior-distal angle subacute; basal slender, armature similar to that of peraeopod 3; merus short, about twice so long as wide, anterior margin convex; carpus twice as long as merus, a little longer than propod; dactyl very slender, as long as basal. *Peraeopod 5,* coxa bilobed, posterior lobe longer but more narrowly rounded than anterior lobe; basal somewhat expanded posteriorly; merus elongate, more than twice as long as basal; carpus relatively short, barely longer than merus; dactyl very slender, half length of propod. *Peraeopod 6,* coxa produced and rounded posteriorly, ventrally rectangular; basal rather narrow, length more than twice width, submarginal row of setae posteriorly; merus slender, twice length of basal; articles 5–7 lost. *Peraeopod 7,* coxa strongly produced posteriorly, posterior-distal angle acute; basal narrowly oval, merus less than twice length of basal; articles 5–7 lost.

Uropod 1, peduncle with two spines on lateral margin and three on median margin, rami narrowly lanceolate, inner as long as peduncle, one-tenth longer than outer. *Uropod 2,* not extending as far back as apices of uropod 1; peduncle two-thirds length of inner ramus; rami narrowly lanceolate, inner ramus very slender apically, with five spines on inner margin; outer ramus about three-quarters as long as inner ramus. *Uropod 3,* peduncle short; rami lanceolate, bearing spines on inner margins, outer ramus one-eighth shorter than inner; rami of all uropods microscopically pectinate. *Telson* linguiform, bearing two setae basally and scattered minute setules dorsally, cleft about one-third of total length, apices not dehiscent.

Allotype, male, 12mm. Sexual dimorphism in this species is greater than is the case in most of the better known species in the genus. Differences between the sexes are shown by the pleon armature, antennae, mandibular palp and possibly the posterior peraeopods.

Pleon, teeth on pleonites 1 and 2 similar in form to those of the female, but less strongly produced, pleonite 3 tooth carinate but not produced distally, the carina being truncate with a small backwardly directed tooth at the posterior-distal extremity. *Antenna 1,* peduncle article 2 two-thirds length of article 1, both articles with transverse rows of short setae on medio-ventral surfaces; article 3 very short; barely longer than wide; flagellum two-and-a-half times length of peduncle, filiform, of 27 articles. *Antenna 2,* four-fifths longer than antenna 1, peduncle articles 3 and 4 with ranks of short setae opposed to those on peduncle of antenna 1; article 4 stouter but just shorter than article 5; flagellum nearly three times length of peduncle, filiform, of 51 articles. *Mandible,* palp slender much longer than body of mandible; article 3 slender, longer than articles 1 and 2 combined, armed with short setae over distal four-fifths of posterior margin. *Peraeopod 7,* basal oval; merus much longer than basal, a little shorter than carpus; propod slender, straight, one-third longer than carpus; dactyl slender, two-fifths length of carpus.

REMARKS. *R. gislii* belongs among those species in which the dorsal armature is restricted to

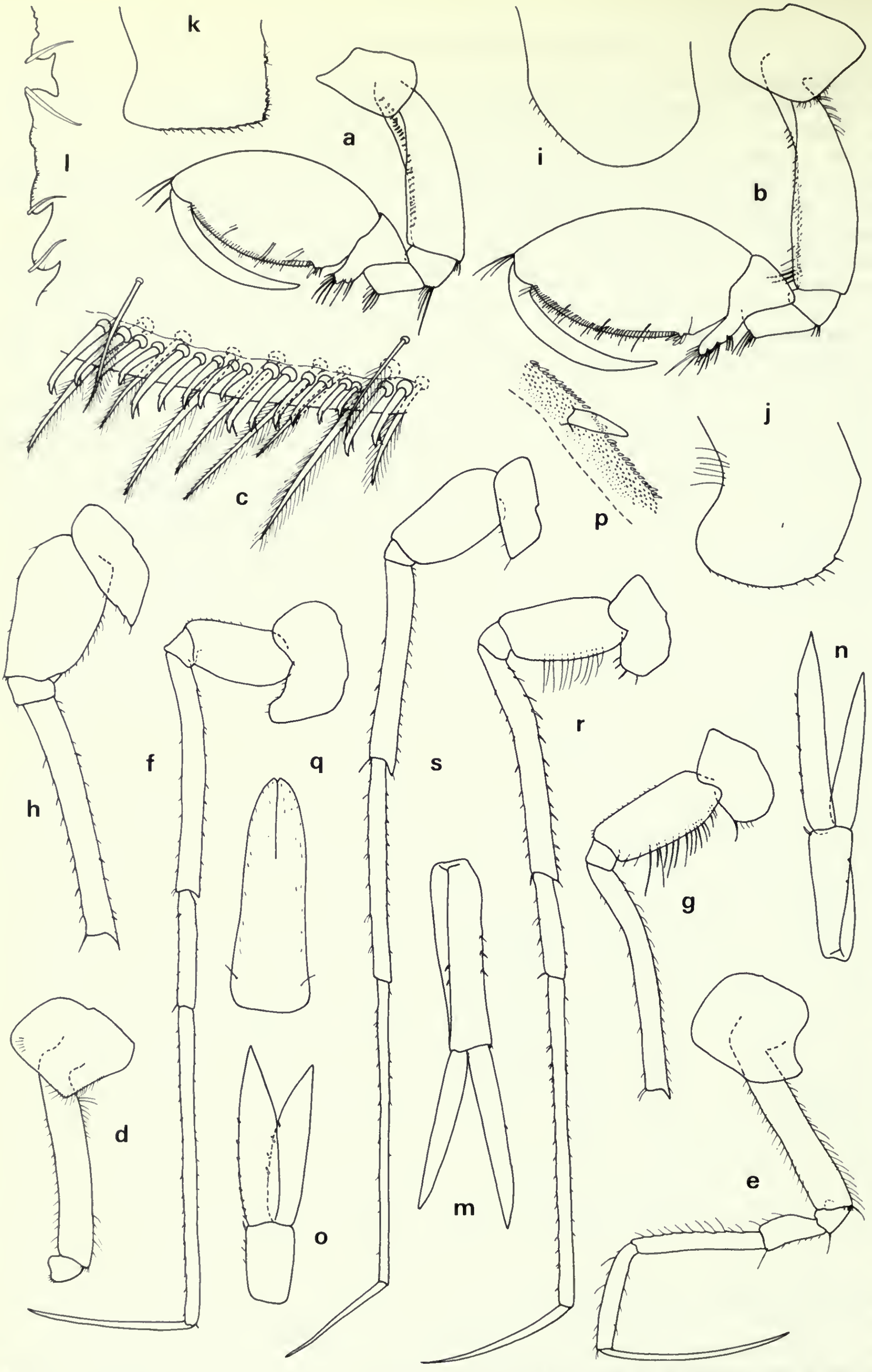

Fig. 8 *Rhachotropis gislii* sp. nov. Holotype, female, 14mm. (a–b) gnathopods 1 & 2; (c) gnathopod 2, detail of palm; (d–h) peraeopods 3–7; (i–k) epimera 1–3; (l) epimera 3, detail; (m–o) uropods 1–3; (p) uropod 3, margin of outer ramus; (q) telson. Paratype female, 13mm. (r) peraeopod 6. Paratype male, 11mm. (s) peraeopod 7.

three, three and one teeth respectively on pleonites 1–3, and which have a weakly produced first coxa.

Only three species of *Rhachotropis* combine an edentate urosomite 1 with a weakly produced coxa 1. Of those, *R. elegans* Bonnier, 1896 and *R. gubilata* Barnard, 1964 are distinguished from the present species by a tridentate pleonite 3. The stout, serrate basal article of peraeopod 7 and broadly rounded epimeron 3 of *R. elegans,* and strong posterior teeth on the basal articles of peraeopods 5–7 and weakly cleft telson of *R. gubilata* afford further means of separating these species from *R. gislii.* The third species, *R. natator* (Holmes, 1908), is a weakly dentate entity, bearing single teeth on pleonites 2 and 3 only. This condition contrasts with that found in *R. gislii* as does the weakly cleft telson. *R. grimaldii* (Chevreux, 1887), which has been regarded as synomymous with *R. elegans* by several authors (Barnard, 1916; Stephensen, 1944*a*; Gurjanova, 1955; Barnard, 1957) differs from *R. gislii* in having a tridentate pleonite 3, strongly produced coxa 1, broadly rounded and strongly serrate epimeron 3, broad peraeopod 7 basal article, and large eyes. The dorsal armature of *R. levantis* and *R. thorkelli* resembles that of *R. gislii* but the former species has a long rostrum, moderately produced and anterior-ventrally rounded coxa 1, broad peraeopod 7 basal article, serrate epimeron 3 and calceolate antennae, while the latter has a dentate urosome, slender basal articles of peraeopods 5–7, and a shallowly cleft telson. *R. anoculata* and *R. luculenta* Barnard, 1969 both have strongly produced first coxae and lack teeth on pleonite 3, although in the former this segment has a prominent posterior margin. *R. anoculata* has calceolate antennae and a more deeply cleft telson than does *R. gislii* while *R. luculenta* differs in having eyes, a long rostrum, calceolate antennae, broad peraeopod 5–6 basal articles and a more deeply cleft telson.

Rhachotropis arii sp. nov.
(Figs. 9–10)

MATERIAL EXAMINED. St. 7709#62 1♂ 10mm, 1♀ 14mm, 1 damaged specimen. Sta. 7709#66 1♂ 12mm, 2♀ 14mm. Sta. 7709#72 4♂ 12mm, 9♀ 6–14mm, 2 juv. 6mm. ALLOTYPE ♀ BM(NH) reg. no. 1978: 230. Sta. 7709#73 1♀ 15mm, 1 damaged specimen. Sta. 7709#85 3♂ 12mm, 1♀ 10mm, 1 juv. 6mm. HOLOTYPE ♂ BM(NH) reg. no. 1978: 229 [carcase and 4 microscope preparations], PARATYPES 1978: 231.

The registered type material has been deposited in the collections of the Zoology Department of the British Museum (Natural History); all remaining material has been retained at the Institute of Oceanographic Sciences.

ETYMOLOGY. Ari Thorbjornsson, younger brother of Gisli.

DESCRIPTION. Holotype male, 12mm. *Pleon,* segments 1 and 2 each slightly humped, with low dorsal tooth; segment 3 carinate, the carina ending in a small posteriorly directed tooth. *Epimera,* first and second rounded; third sub-rectangular, not serrate on posterior or ventral margins. *Urosome,* first segment carinate, the carina produced posteriorly into a tooth.

Head, rostrum short, spatulate; eyelobes produced, rounded, extending almost as far as rostrum; post-antennal angle rounded; epistome not produced beyond upper lip. *Antenna 1,* filiform, as long as head, peraeon and pleon combined; first article of peduncle rather stout, longer than articles 2 and 3 combined; article 3 short, length hardly greater than width; flagellum of 38 articles, about three times length of peduncle, basal fifth somewhat expanded, conjoint, bearing large numbers of long, filamentous aesthetes; accessory flagellum minute. *Antenna 2,* subequal in length to body; distal articles of peduncle bearing many short spine-setae dorso-medially; article 5 very slender, longer than articles 1–4 combined: flagellum filiform, rather less than twice as long as peduncle, of 42 articles, each article bearing a sub-terminal cluster of fine setae. *Upper lip,* rounded, bearing corona of fine setae. *Mandible,* incisor process strong, heavily chitinized, with single distal tooth and long cutting edge; lacina mobilis of left mandible with six blunt teeth, that of right bidentate; spine row with three stout pectinate spines; molar process columnar, triturating surface strongly

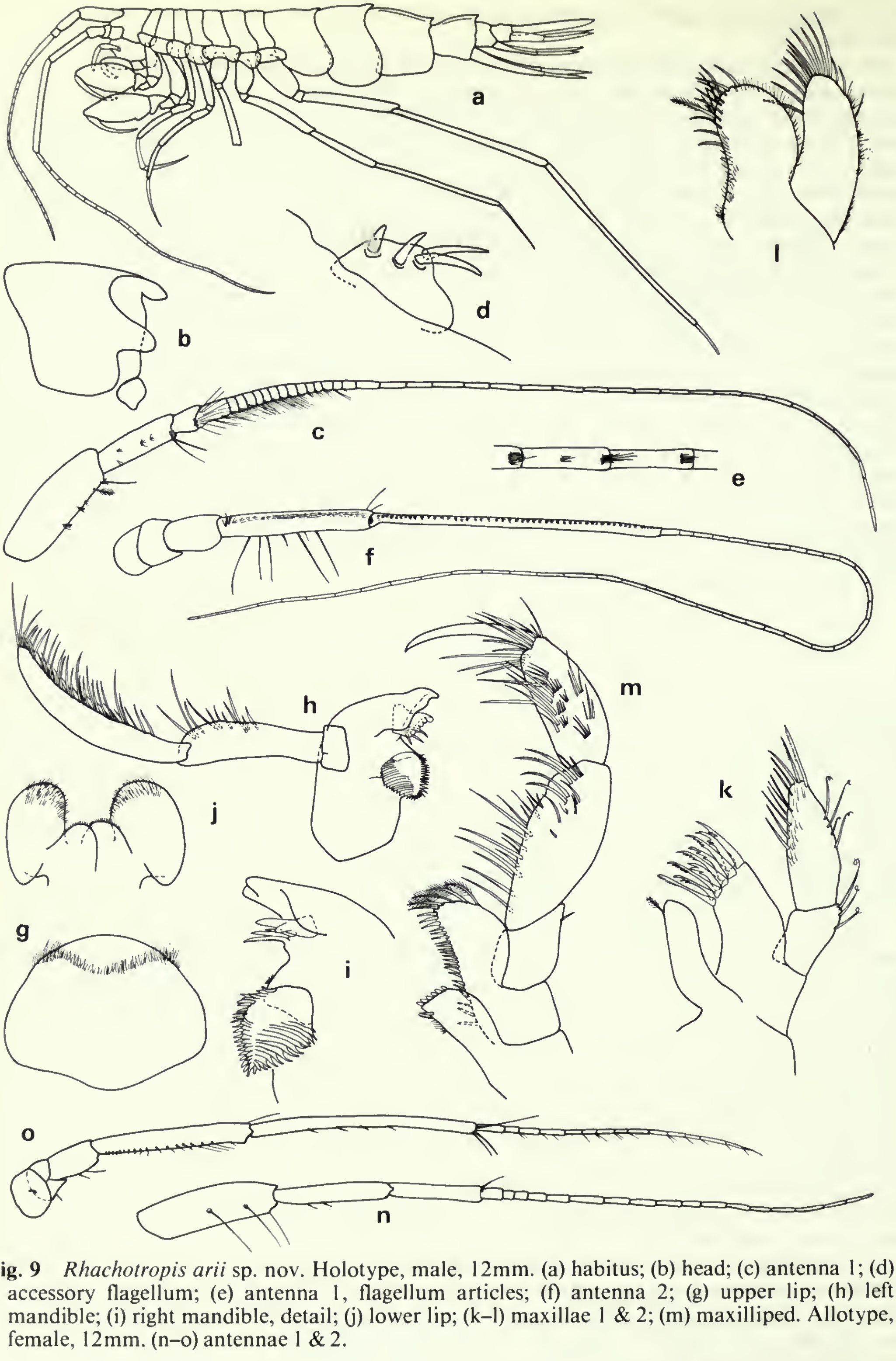

Fig. 9 *Rhachotropis arii* sp. nov. Holotype, male, 12mm. (a) habitus; (b) head; (c) antenna 1; (d) accessory flagellum; (e) antenna 1, flagellum articles; (f) antenna 2; (g) upper lip; (h) left mandible; (i) right mandible, detail; (j) lower lip; (k–l) maxillae 1 & 2; (m) maxilliped. Allotype, female, 12mm. (n–o) antennae 1 & 2.

toothed and ridged; palp long, third article as long as body of mandible, falciform, posterior margin strongly armed with slender spines and stout setae over most of length. *Lower lip,* inner lobes prominent. *Maxilla 1,* inner plate slender, distally rounded, bearing a single, subterminal plumose seta; outer plate with nine slender dentate or pectinate spines; second article of palp narrowly rounded distally, both margins armed with setae, those of outer margin tipped with spiral filaments. *Maxilla 2,* inner plate broad, rounded, armed with single plumose seta and two ranks of slender spines medio-distally; outer plate as long as inner but barely half the width, armed distally with long slender spines. *Maxilliped,* inner plate short, apically transversely truncate, with six stout spine teeth; outer plate small, hardly extending beyond apex of first palp article, armed with plumose setae distally and slender spine-teeth medially; palp well developed, second article longest, second and third articles strongly setose and spinose, fourth article slender, curved, subequal in length to third article.

Gnathopod 1, coxa rather weakly produced, anterior margin shorter than basal margin, anterior-ventral angle rounded; basal expanded distally; carpus short, posterior lobe well developed, strongly setose; propod oval, palm three-quarters length of posterior margin, armature similar to that of *R. grimi;* dactyl slender, as long as palm. *Gnathopod 2,* coxa rounded, somewhat produced anteriorly; carpus short, posterior lobe extending to palmar angle of propod, strongly setose; propod similar to that of gnathopod 1 but slightly larger. *Peraeopod 3,* coxa small, rounded, anteriorly produced; basal slender; merus half length of carpus; carpus and dactyl slender, subequal, a little longer than propod. *Peraeopod 4,* coxa produced anteriorly, broadly rounded, ventral margin concave, posteriorly excavate, posterior-ventral angle sub-acute; basal slender; merus just more than half length of carpus; propod seven-eighths length of carpus; dactyl very slender, one-fifth longer than carpus. *Peraeopod 5,* coxa bilobed, lobes equal; basal narrowly oval; merus curved, more than twice as long as basal; distal articles lost. *Peraeopod 6,* coxa strongly produced posteriorly, basal narrowly oval; merus and carpus gently curved, subequal; propod elongate, equal in length to merus and carpus combined; dactyl curved, very slender, three-eighths length of propod. *Peraeopod 7,* immensely elongate, length exceeds total length of animal; coxa posteriorly produced, lobe distally truncate; basal oval, just more than half length of merus; carpus, three-quarters as long again as merus; propod extremely slender, half as long again as carpus; dactyl damaged, but apparently short, probably not more than one-fifth length of propod.

Uropod 1, rami narrowly lanceolate, subequal, two-thirds length of peduncle. *Uropod 2,* not quite reaching apex of uropod 1; rami narrowly lanceolate, inner nine-tenths length of peduncle, outer seven-tenths. *Uropod 3,* peduncle rather stout, medial margin strongly spinose; rami subequal, three-fifths longer than peduncle, margins spinous and pectinate. *Telson,* linguiform with two setae basally and scattered minute setules dorsally, cleft for one-tenth of length, apices acute, dehiscent.

Allotype, female, 12mm. *Pleon,* segment 3 with low carina ending in small acute tooth. *Urosome,* segment 1 with low posteriorly dentate carina. *Antenna 1,* first peduncle article stout; second and third slender, together half as long again as first, third three-quarters length of second; flagellum a little longer than peduncle, of 17 articles; accessory flagellum minute. *Antenna 2,* subequal in length to antenna 1; peduncle article 5 slender, nearly as long as articles 1–4 combined; flagellum two-fifths length of peduncle, of 15 articles.

REMARKS. *R. arii* belongs to those species having single median teeth on pleonites 1–3 and urosomite 1, and a weakly produced first coxa.

During a redescription of *R. gracilis* Bonnier, 1896 (Thurston, in prep.), it became apparent that several slight but apparently significant differences exist between the present specimens and Bonnier's type material. The easiest means of separation lies in the form of coxa 2 and coxa 4. Coxa 2 of *R. arii* is evenly rounded anteriorly while that of *R. gracilis* is distally truncate. Coxa 4 of the latter species is rectangular, and lacks the posterior-distal projection found in *R. arii.* The new species is characterized by a very short accessory

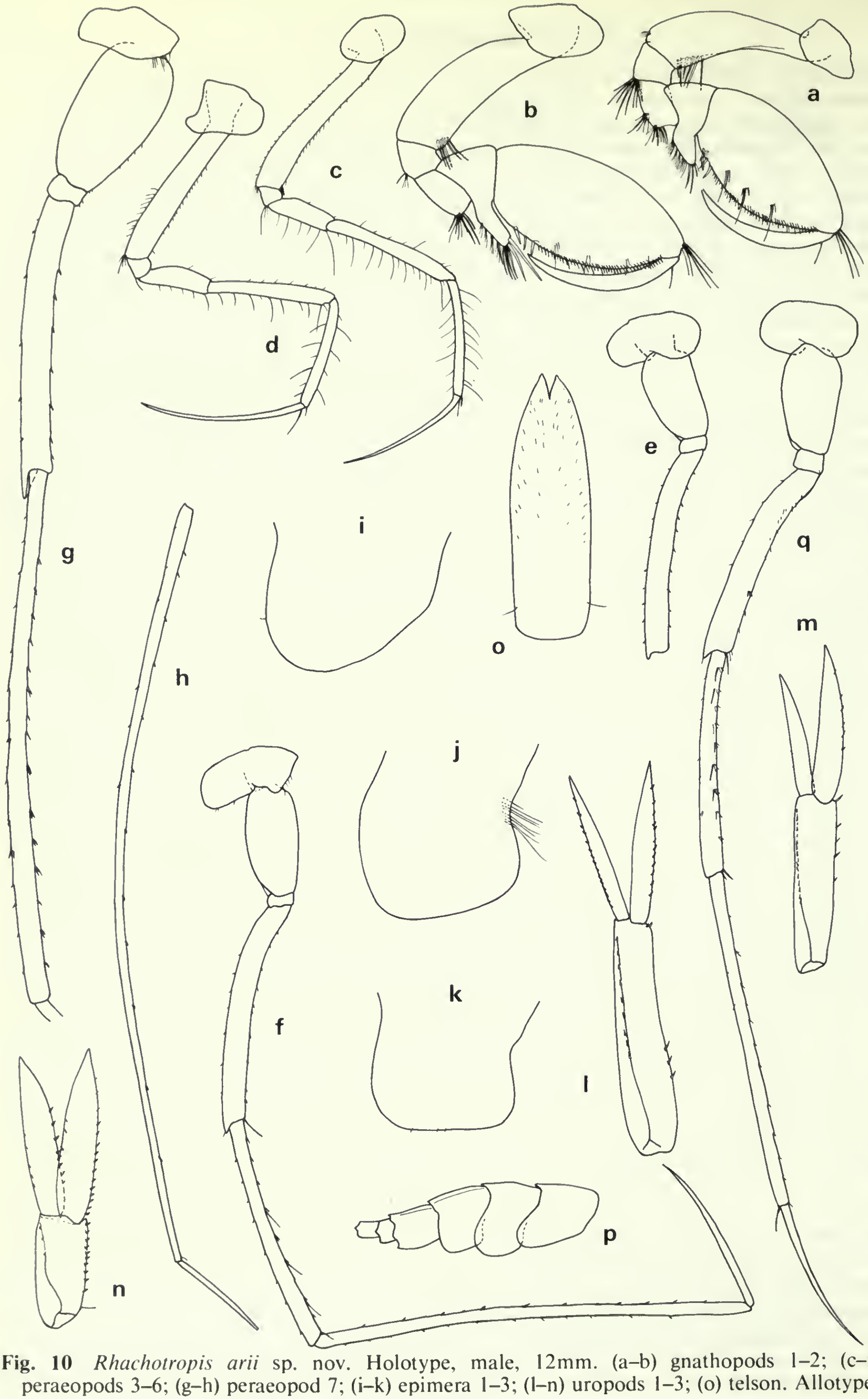

Fig. 10 *Rhachotropis arii* sp. nov. Holotype, male, 12mm. (a–b) gnathopods 1–2; (c–f) peraeopods 3–6; (g–h) peraeopod 7; (i–k) epimera 1–3; (l–n) uropods 1–3; (o) telson. Allotype, female, 12mm. (p) pleon and urosome; (q) peraeopod 5.

flagellum armed with four spines, a weakly produced upper lip, maxilla 1 inner plate slender and armed with a single plumose seta, and epimeron 3 smooth posterior-distally. In contrast, *R. gracilis* has an accessory flagellum which is longer than wide and armed with a single long setae, a relatively strongly produced upper lip, maxilla 1 inner plate oval and bearing two plumose setae distally, and epimeron 3 crenelate posterior-distally. In male specimens the structure of antenna 1 peduncle differs, the second article being three-fifths the length of the first in *R. arii* but subequal to it in *R. gracilis.* These differences are not large, and future research may show them to be of intra-specific value only. Until that time I prefer to maintain the two entities as separate species.

Three previously described species of *Rhachotropis,* in addition to *R. gracilis,* have each pleonite armed only with a single median tooth. Both *R. faeroensis* Stephensen, 1944 and *R. ludificor* Barnard, 1967 are distinguished from *R. arii* by their strongly produced first coxae. In addition, *R. faeroensis* has a rostrum half as long as the first peduncle article of antenna 1, epimeron 3 evenly rounded and posterior-distally serrate, calceolate antennae and the basal article of peraeopod 7 with a sub-acute posterior-distal lobe. Further characters separating *R. arii* and *R. ludificor* lie in the longer rostrum, rounded and serrate epimeron 3, shorter and more deeply cleft telson and produced posterior-distal lobe of peraeopod 7 basal article of the latter. *R. portoricana* Barnard, 1964 has a strongly deflexed rostrum, edentate urosomite 1 and lobate peraeopod 7 basal article, all characters not found in *R. arii.*

Apart from *R. gracilis,* two other species combine a dentate urosomite 1 and weakly produced coxa 1. *R. anomala* Barnard, 1916 is similar in many characters to *R. arii* but can be distinguished by the lack of teeth on pleonites 1 and 3 and the non-dehiscent apices of the telson.

Two other species have weakly produced first coxae. *R. thorkelli* has tridentate pleonites 1 and 2, and rectangular rather than oval basal articles on peraeopods 5–7. *R. natator* resembles *R. arii* but lacks median teeth on pleonite 1 and urosomite 1, and is further distinguished by the form of the telson, the slender propods of gnathopod 1 and 2, and the acute anterior-distal angle of coxa 2.

Acknowledgements

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Abyssal benthic Amphipoda (Crustacea) from the East Iceland Basin

2. *Lepechinella* and an allied new genus

Michael H. Thurston
Institute of Oceanographic Sciences, Wormley, Godalming, Surrey

Introduction

R.R.S. *Discovery* Cruise 39 took place in April–May 1971 and was concerned with biological investigations at 60° N 20° W and 53° N 20° W. The main purpose of the cruise was a study of vertical distribution and migration of the zooplankton and nekton. Secondary objectives included an investigation of the benthic fauna, and to this end epibenthic sledge hauls were made at both stations. This paper deals with the dexaminid genus *Lepechinella* and a closely related genus obtained from five hauls at the northern station. It follows a report on species of the eusirid genus *Rhachotropis* (Thurston, 1980).

Material and methods

For station data and methods see previous paper (Thurston, 1980 p. 44–45).

Small circles in some of the illustrations indicate the bases of setae either deliberately omitted for clarity of the underlying structure (particularly coxae and gnathopods) or lost prior to examination.

Systematics

Over 3500 gammarids representing about 120 species were obtained from the five sledge hauls. Although the sledge had no opening/closing facility, contamination was minimal. Only a very small proportion of the total catch was clearly of midwater origin. More than half of the benthic species distinguished appear to be undescribed. Four species are discussed herein, three belonging to *Lepechinella* and represented by a total of 340 specimens, and the fourth to a new genus represented by 93 specimens. Together these four species account for 12·2% of the total number of specimens obtained.

The bottom in the area investigated consisted of dark grey-brown mud together with small quantities of sand, stones, clinker and pteropod shells.

Variation. Barnard (1973) has discussed speciation in *Lepechinella,* pointing out that many of the interspecific characters currently used in the genus are quantitative rather than qualitative. Most species are known from few specimens so that the degree of intraspecific variation is unknown. The volume of material in the present collection has made possible an initial insight into this problem, in that a common pattern of sexual dimorphism and allometric growth can be seen in the three species of *Lepechinella* studied.

As is true of the vast majority of amphipod species bearing dorsal teeth or carinae, these projections in *Lepechinella* become relatively more prominent with increasing size. In juveniles of both sexes, all females and juvenile males, dorsal teeth tend to be rather slender and upstanding. As males develop towards maturity, the bases of these teeth become elongated along the dorsal midline of the segment, and the teeth themselves become more decumbent. A state is reached in fully developed specimens in which body segments, particularly the posterior peraeonites and the pleonites, become carinate, with each carina ending in a posteriorly directed tooth. Concomitant with these changes is the development of a dorsal tooth on urosomite 3. Terminal males also show marked modifications of the

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antennae. The second peduncle article of antenna 1 and the fourth peduncle article of antenna 2 become elongate and, together with the third peduncle article of antenna 1, develop many dense bundles of sensory setae.

Characters of the rostrum have been used previously as a means of species separation. However, study of the species of *Lepechinella* in this collection has shown gross intraspecific variation in both length and form. Within a single species the rostrum may be long or short, deflexed, reflexed or straight. Cephalic teeth, particularly the first, show variation of a similar kind though lesser extent. The degree and nature of variation of general body setation or spination and lateral setal rows on the epimera is poorly known. In the present collection there appears to be a wide degree of intraspecific variation. However, this armature is extremely brittle, at least in some species. It is likely to be radically affected by the processes of retrieval and the removal of adhering debris which is so frequently necessary to reveal even gross morphology. The apparent absence of body setation, both general and epimeral, from some described species should be treated with reserve. Absolute confirmation of presence or absence will require careful examination of appreciable numbers of clean, undamaged specimens.

Lepechinella helgii sp. nov.
(Figs. 1–3)

MATERIAL EXAMINED. Sta. 7709 # 62 3 ovig. ♀ 7–9 mm, 1 ♀ 9mm; Sta. 7709 # 66 3 ♀ 5–7 mm, 1 intersex 8 mm, 2 damaged specimens; Sta 7709 # 72 13 ♂ 7–8 mm, 6 ovig. ♀ 7–8 mm, 28 ♀ 5–9 mm, 19 juv. 3–6 mm, 3 intersex 7–8 mm; Sta. 7709 # 73 33 ♂ 7–8 mm, 9 ovig. ♀ 7–9 mm, 60 ♀ 5–9 mm, 50 juv. 3–6 mm, 19 damaged specimens, HOLOTYPE ♀ ovig. B.M.(N.H.) reg. no. 1978: 232 [carcase and 3 microscope preparations], ALLOTYPE 1978: 233, 9 PARATYPES 1978: 234; Sta 7709 # 85 2 ♀ 8 mm.

The registered type material is deposited in the Zoology Department of the British Museum (Natural History); all the remaining material has been retained at the Institute of Oceanographic Sciences.

ETYMOLOGY. Helgi, youngest son of Njal Thorgeirsson, Burnt Njal.

DESCRIPTION. Holotype, female, 9 mm, from Sta. 7709 # 73. *Peraeon,* all segments dorsally dentate, teeth 30–40% of height of corresponding segment: peraeonites 1 and 7 with two teeth: peraeonites 2–6 with one tooth near posterior margin; small nodules anterior to teeth on peraeonites 5–7. *Pleon,* each segment with long inclined tooth near posterior margin and two upright projections anterior to main tooth; accessory teeth 40–50% of length of main tooth. *Epimera,* all with posterior-distal tooth separated by a sinus from strongly convex posterior margin; tooth and sinus, smallest on epimeron 1, largest on epimeron 3; each epimeron with lateral setal row. *Urosome,* first segment produced into strong, inclined tooth at posterior margin. *Body,* moderately setose.

Head, setose; rostrum slightly upturned, 70% of length of first article of antenna1; first cephalic tooth slender, 35% of length of rostrum; second cephalic tooth broader and rather shorter than first. *Antenna 1,* just shorter than body; first article of peduncle 55% of length of second; third article 20% of length of second; flagellum 1·5 times length of peduncle; accessory flagellum short, tapering. *Antenna 2,* subequal to antenna 1; first four peduncle articles combined 80% of length of fifth article; flagellum as long as peduncle articles 1–4. *Upper lip,* bilobate. *Mandible,* incisor process dentate; lacina mobilis of left mandible dentate, laminar, that of right bluntly dentate, teeth in two rows; molar ridged, triturative; palp as long as body of mandible, first article 25%, third article 35% of length of second article. *Lower lip,* inner lobes broad. *Maxilla 1,* inner plate small, slender with two stout plumose setae apically; outer plate with eleven dentate spine teeth distally; palp, second article expanded distally, seven spine teeth and one spine on nearly transverse distal margin. *Maxilla 2,* inner plate shorter and much more slender than outer. *Maxilliped,* outer plate ovo-rectangular, fifteen spines and spine teeth medially and distally; palp weak, second article slender, as long as third and fourth articles combined.

Gnathopod 1, coxa strongly bifid, marginally setose; propod suboval, 70% of length of carpus, palm gently convex, shorter than posterior margin of propod, palmar angle marked by single stout spine. *Gnathopod 2,* coxa tapering, distally slender; distal articles longer than those of gnathopod 1; propod 60% of length of carpus, margins almost parallel, palm 70% of length of posterior margin. *Peraeopod 3,* coxa strongly produced anterior-distally; carpus and propod subequal, shorter than merus, longer than dactyl. *Peraeopod 4,* coxa bifid, posterior lobe obsolete; distal articles similar to those of peraeopod 3. *Peraeopod 5,* coxa produced at anterior-ventral corner, projection slightly shorter than that of coxa 4; merus and propod subequal, shorter than carpus, longer than dactyl. *Peraeopod 6,* coxa with small triangular projection at anterior-ventral corner; distal articles similar to those of peraeopod 5. *Peraeopod 7,* coxa with posterior-distal angle acute; merus slightly shorter than propod, otherwise distal articles similar to those of peraeopod 5.

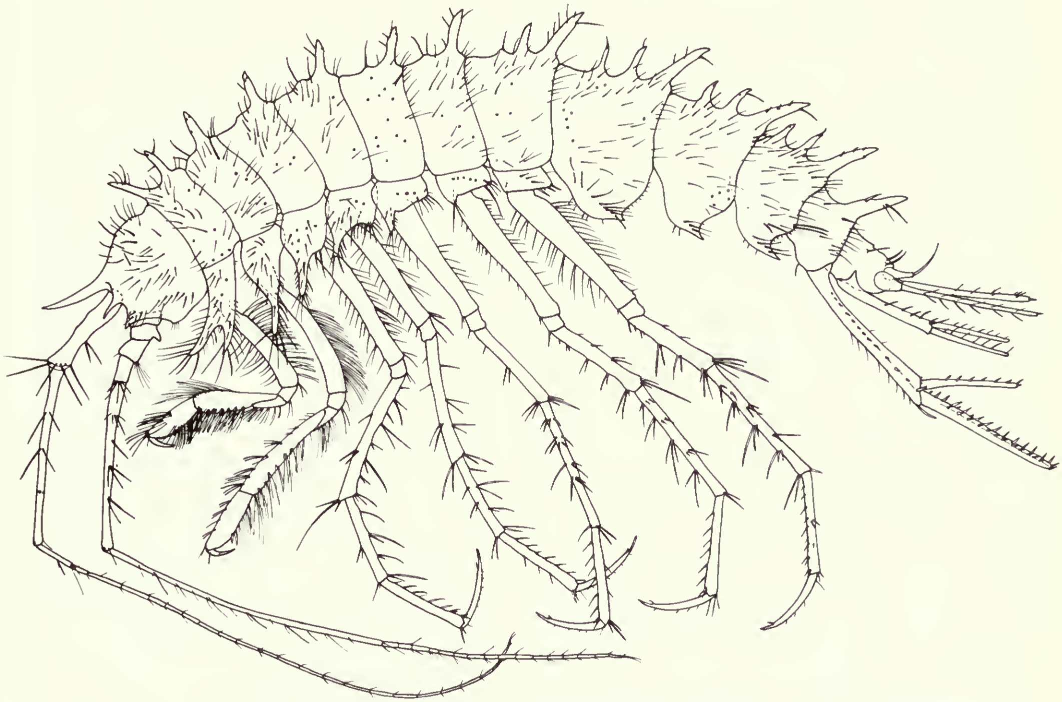

Fig. 1. *Lepechinella helgii* sp. nov. Holotype, female, 9 mm.

Uropod 1, outer ramus not stout, 85% of length of peduncle, spinous; inner ramus 65% of length of outer. *Uropod* 2, not quite reaching apex of inner ramus of uropod 1; rami, slender, subequal, 75% of length of peduncle. *Uropod 3,* extending about as far as uropod 2; peduncle very short; rami slender, subequal. *Telson,* short, length and breadth equal; cleft 40% of length, cleft nearly semicircular; apices bifid, each bearing a long stout spine.

VARIATION. Sexual variation is apparent in the dorsal armature of the pleon and in the third epimera. In adult males the main pleonal teeth are less upright and more carinate, the accessory teeth are rather shorter, and the posterior-distal tooth and sinus of epimera 3 are less prominent than is the case in female specimens. Immature males resemble females in these characters. Juveniles less than about 3·5 mm long have only a single accessory tooth on each of pleonites 1–3. Hatchlings are about 1·5 mm long, and lack rostrum and dorsal armature. The rostrum of adult and subadult individuals is generally straight and about 70% as long as the first peduncle article of antenna 1. A minority of specimens have slightly longer or appreciably shorter rostrums which may be gently upcurved or somewhat deflexed.

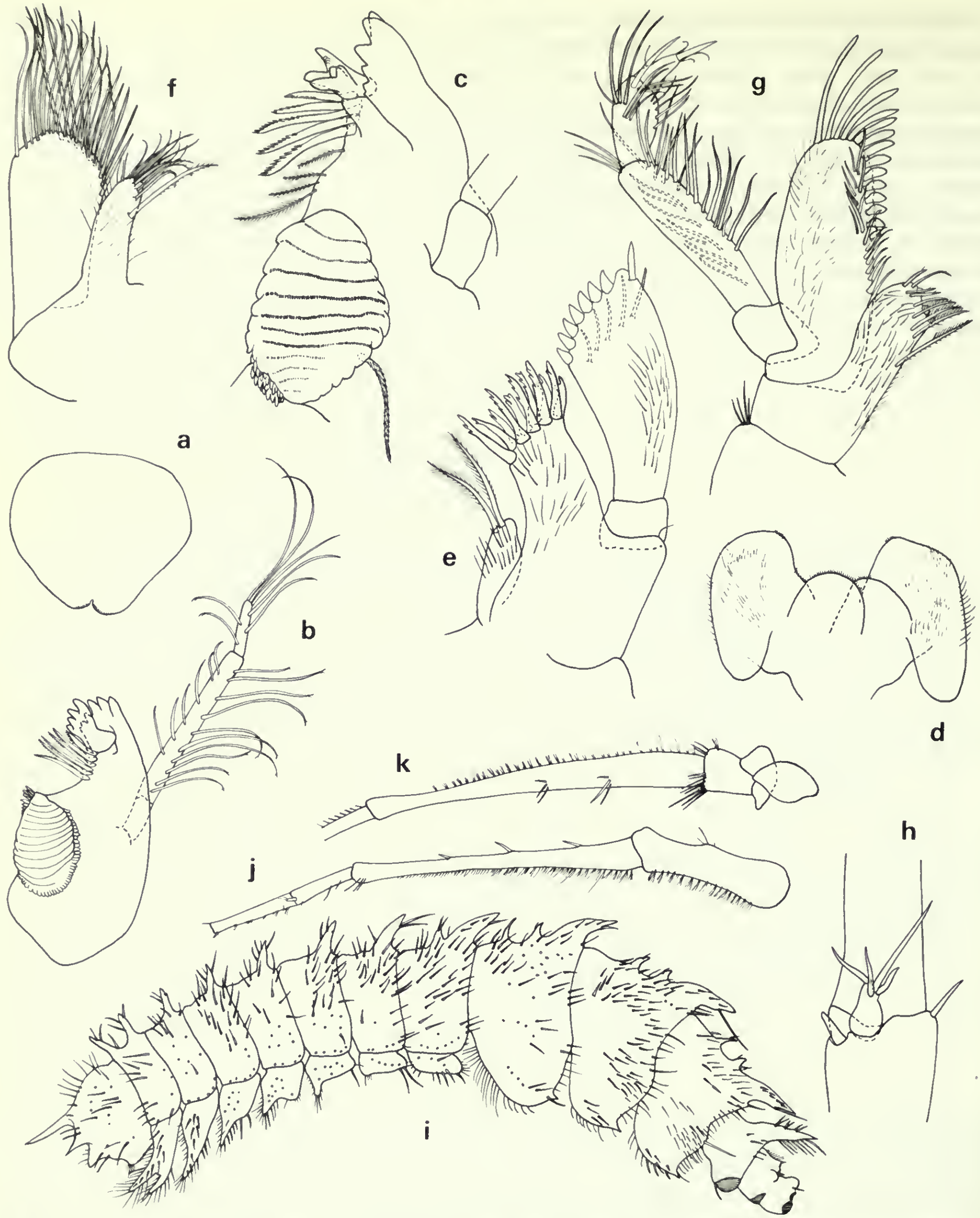

Fig. 2. *Lepechinella helgii* sp. nov. Holotype, female, 9 mm. (a) upper lip; (b) left mandible; (c) right mandible, detail; (d) lower lip; (e–f) maxillae 1 & 2; (g) maxilliped; (h) accessory flagellum. Allotype, male, 8 mm (i) body; (j–k) antennae 1 & 2.

Remarks. Barnard (1973) has provided a phyletic key to the species of *Lepechinella*. *L. helgii* falls into the category characterized by strongly dentate peraeonites, a bidentate peraeonite 1, and a bifid coxa 1. Other species possessing these basic characters are *L. chrysotheras* Stebbing, 1908, *L. arctica* Schellenberg, 1926, *L. turpis* Barnard, 1967, *L. eupraxiella* Barnard, 1973 and *L. manco* Barnard, 1973. Most species of *Lepechinella* are known only from single localities and few specimens, and the nature and degree of intraspecific variation is poorly understood. Because of or despite these limitations, the majority of species within the genus seem sufficiently distinct to be fairly readily separable. This is not true, however, of the six species in the *L. chrysotheras* group. All of these are closely similar in body morphology and differ only in small and rather subtle characters. Clarification of *L. chrysotheras, L. arctica* and *L. eupraxiella* and more material of the other species from additional localities will be required to understand the true nature of the components of this group.

The following analysis is based largely on characters of the dorsal armature, coxae, epimera and uropods. Peraeonite 7 in *L. helgii* has a strong accessory tooth anterior to the main dorsal tooth, thus resembling *L. turpis.* In *L. chrysotheras, L. arctica* and *L. manco* an accessory tooth is present, but small, being about 20% of the height of the main tooth rather than 50% as is the case in the other two species. Only in *L. eupraxiella* is there no trace of a tooth present. Two accessory teeth are present on pleonites 1–3 in *L. helgii, L. chrysotheras, L. manco* and *L. turpis.* The teeth are large in the first and last of these species, and smaller in the other two. *L. arctica* and *L. eupraxiella* have only a single accessory tooth on these segments. The apparent differences in pleonal armature apply only to adult individuals. In the present species, and in *L. turpis* if all Barnard's material is conspecific, small juveniles have either a single tooth moderately developed or both teeth vestigial.

The size and shape of the sinus above the posterior-distal tooth of epimeron 3 appears to offer a means of separating species in this complex, *L. eupraxiella* being particularly characteristic in this respect. *L. helgii* suggests that the situation is complex, however, as in this species sexual dimorphism occurs. The sinus of the female is much deeper and wider than in the male. The presence or absence of lateral rows of setae on the epimera is at present of doubtful value as a diagnostic character as the situation is poorly known for several species. In addition, the setae seem particularly vulnerable to abrasion. This is also a problem with the general body setation or spination. Only *L. helgii* and *L. manco* are known to be heavily armed in this respect.

With the exception of *L. turpis* all species have coxa 1 cleft about 25% of the length. Even in *L. turpis,* however, the difference is not clear cut, as presumed juveniles have a more deeply bifid coxa 1 than do adults. Coxa 3 is distinctly bifid in *L. chrysotheras, L. eupraxiella* and *L. manco.* In these three species the posterior lobe is acute though small, whereas in the other three species this lobe is vestigial and rounded or absent. *L. helgii* and *L. turpis* have the posterior-distal lobe of coxa 4 obsolete, whereas in the other four species it is acutely produced to a varying degree. The coxae of peraeopods 5–7 are rather uniform among all species except *L. eupraxiella.* In that species, coxa 5 is bifid with a very long acute anterior lobe and coxa 6 has the same lobe bent forward and strongly hooked.

Uropod 1 of *L. helgii* has the inner ramus only 65% as long as the outer ramus, whereas in *L. chrysotheras, L. arctica, L. turpis* and *L. manco* the rami are not markedly different in length. The condition in *L. eupraxiella* is obscure as the uropods of that species are poorly known. The rami of uropod 2 in *L. helgii* are subequal, in *L. chrysotheras* the outer ramus is a little shorter than the inner, while in *L. manco* the outer ramus is less than 70% of the length of the inner ramus.

Lepechinella grimi sp. nov.
(Figs. 4–6)

MATERIAL EXAMINED. Sta 7709 # 62 1 ♂ 11 mm, 1 ♀ 9 mm, 3 damaged specimens; Sta. 7709 # 66 1 juv. 4 mm; Sta. 7709 # 72 3 ♂ 8–12 mm, 1 ♀ 9 mm, 1 juv. 4 mm, 2 damaged specimens, HOLOTYPE ♂ B.M.(N.H.) reg. no. 1978: 235 [carcase and 3 microscope preparations], PARATYPES 1978: 236; Sta. 7709 # 73 1 ♀ 8 mm, 2 juv. 7–9 mm, 1 damaged specimen; Sta. 7709 # 85 2♂ 10 mm, 1 ♀ 9 mm, 1 juv. 5 mm.

Material from Sta. 7709 # 72 has been deposited in the collections of the Zoology Department of the British Museum (Natural History); the specimens from other catches are housed at the Institute of Oceanographic Sciences.

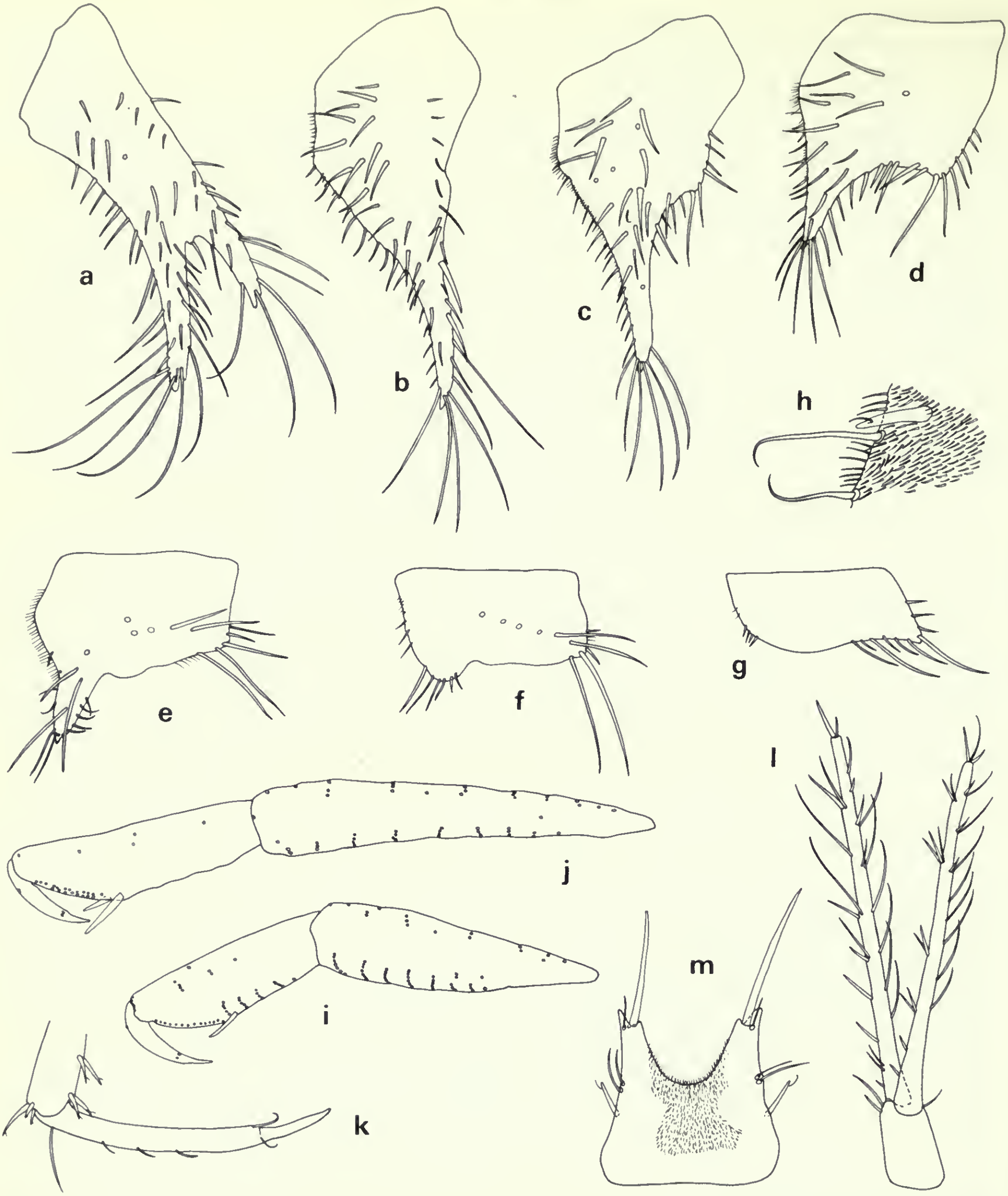

Fig. 3. *Lepechinella helgii* sp. nov. Holotype, female, 9 mm. (a–g) coxae 1–7; (h) coxa 3, detail; (i–j) gnathopods 1–2; (k) peraeopod 4, dactyl; (l) uropod 3; (m) telson.

ETYMOLOGY. Grim, second son of Burnt Njal.

DESCRIPTION. Holotype, male, 12 mm, from Sta. 7709 # 72. *Peraeon,* all segments dorsally dentate, teeth 15–20% of height of corresponding segments; peraeonite 1 with two upright teeth; peraeonites 2 and 3 each with single upright teeth; peraeonites 4–7, teeth carinate and posteriorly directed. *Pleon,* all segments dorsally carinate, each carina terminating in an acute, posteriorly directed tooth. *Epimera,* strongly convex posteriorly, each with well-developed posterior-distal tooth; epimera 1–2 with lateral setae. *Urosome,* segment 1 strongly produced posterior-dorsally, urosomite 3 with acute posterior tooth. *Body* setose and scabrous.

Head, setose, rostrum curved, 30% of length of first peduncle article of antenna 1; first cephalic tooth long, slender, 35% longer than rostrum; second cephalic tooth acute, 40% of length of first, separated dorsally from head margin by small sinus. *Antenna 1,* just longer than peduncle of antenna 2; first article of peduncle 25% of length of second; third article 17% of length of second; second and third articles with setal bundles posteriorly; accessory flagellum elongate, breadth 30% of length. *Antenna 2,* longer than body; third and fourth articles with setal bundles anteriorly; fifth article of peduncle very slender, longer than articles 1–4 combined; flagellum about as long as flagellum of antenna 1. *Upper lip,* asymmetrically cleft, lobes rounded. *Mandible,* incisor process dentate; lacina mobilis of left mandible coarsely dentate, that of right mandible with two plates each with serrate cutting edge; molar triturative, armed with rows of very small teeth; palp just longer than body of mandible, article 1 30% of length of article 3, article 2 twice as long as article 3. *Lower lip,* inner lobes well developed. *Maxilla 1,* inner plate with two plumose setae; outer plate with ten dentate spine teeth; palp, second article distally expanded and obliquely truncate, distal margin with seven blunt spine teeth. *Maxilla 2,* inner plate narrower and slightly shorter than outer. *Maxilliped,* inner plate elongate, rather slender, bearing three blunt spine teeth distally; outer plate slender, seventeen stout spine teeth and setae on medial and distal margins; palp articles 3 and 4 subequal, together as long as article 2.

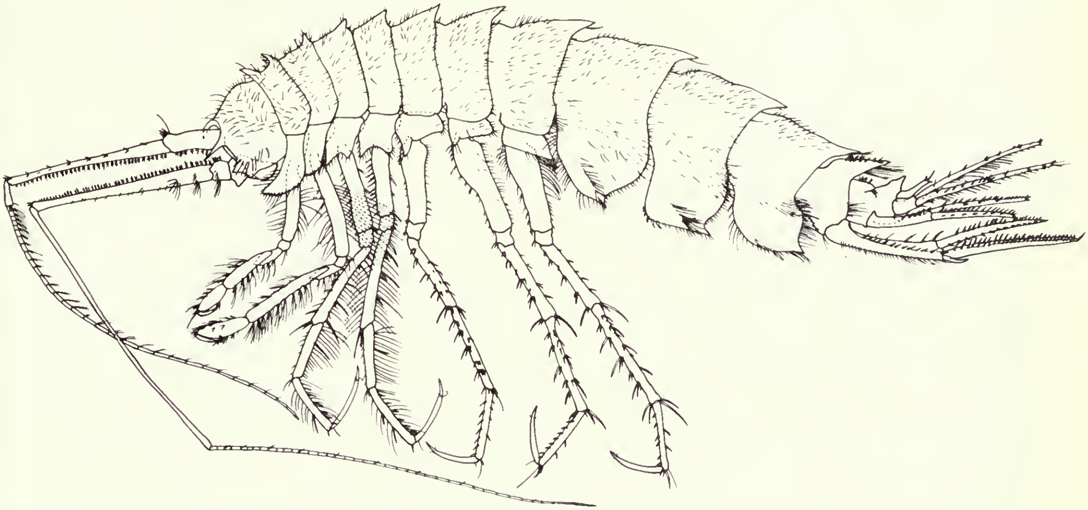

Fig. 4. *Lepechinella grimi* sp. nov. Holotype, male, 12 mm.

Gnathopod 1, coxa slipper-shaped, not bifid, convex distal margin serrate, anterior and distal margins armed with stout setae; propod stout, 65% of length of carpus, palm shorter than posterior margin. *Gnathopod 2,* coxa setose marginally, distally tapering, anterior margin convex, distal margin oblique and serrate; propod 55% of length of carpus, palm and posterior margin subequal. *Peraeopods 3–4,* coxae bifid, lobes acute, anterior lobe longer than posterior, anterior margin convex. *Peraeopod 5,* coxa anterior lobe as long as that of peraeopod 3, rounded posterior-distally. *Peraeopod 6,* anterior lobe of coxa weak, rounded, posterior distal angle of coxa just sub-acute. *Peraeopod 7,* coxa with acutely produced posterior-distal angle.

Uropod 1, outer ramus and peduncle subequal; inner ramus 80% of length of outer. *Uropod 2,* outer ramus 85% of length of inner. *Uropod 3,* peduncle very short; rami subequal, nearly five times length of peduncle, extending beyond uropod 2; outer ramus with minute

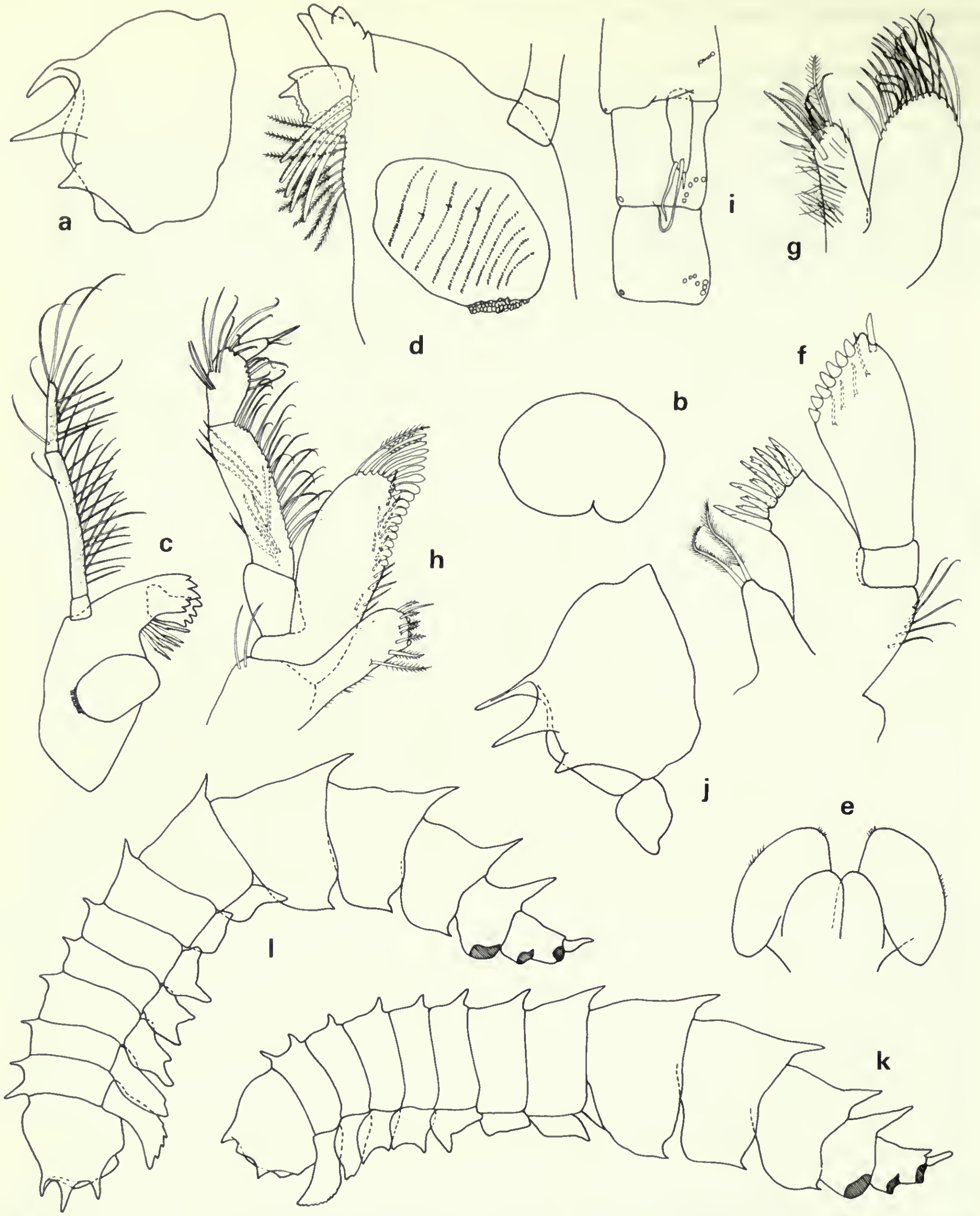

Fig. 5. *Lepechinella grimi* sp. nov. Holotype, male, 12 mm. (a) head; (b) upper lip; (c) left mandible; (d) right mandible, detail; (e), lower lip; (f–g) maxillae 1–2; (h) maxilliped; (i) accessory flagellum. Male, 11 mm. (j) head. Male, 8 mm. (k) body. Juvenile, 5 mm. (l) body.

second article. *Telson,* cleft 65% of length, lobes divergent, each with one long and two short spines subapically, apices acute.

VARIATION. Sexual dimorphism of a pattern apparently common to most if not all species of *Lepechinella* is manifest in the antennae and the dorsal carination (see p. 69). Sexually mature males have a large, sub-erect, conical tooth in urosomite 3. In females and sub-adult males this tooth is much smaller, and in juveniles is obsolete.

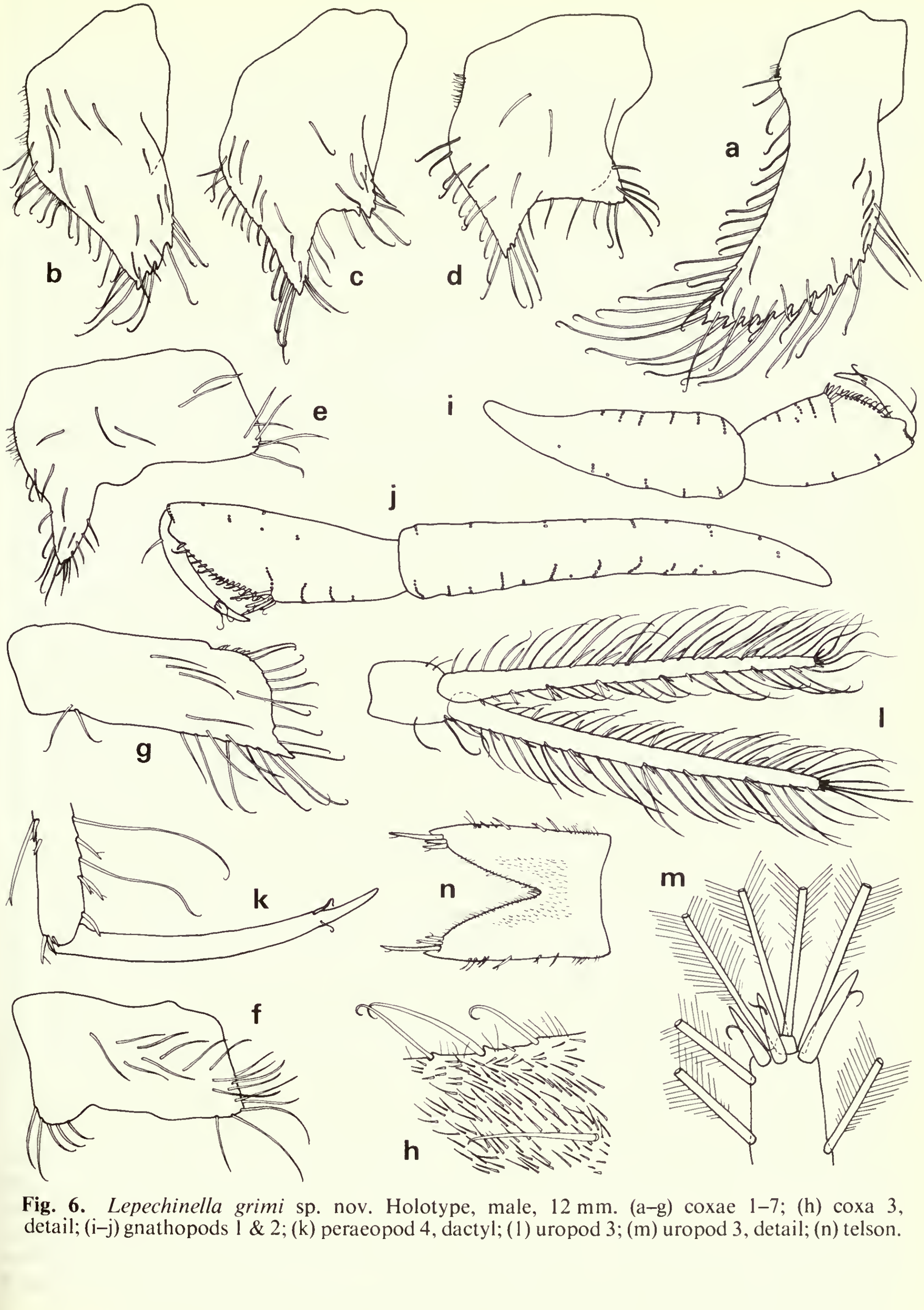

Fig. 6. *Lepechinella grimi* sp. nov. Holotype, male, 12 mm. (a–g) coxae 1–7; (h) coxa 3, detail; (i–j) gnathopods 1 & 2; (k) peraeopod 4, dactyl; (l) uropod 3; (m) uropod 3, detail; (n) telson.

The condition of the rostrum and cephalic teeth is very variable. No two specimens are exactly alike although the normal configuration would appear to be a first cephalic tooth acute and half or slightly less as long as the head excluding the rostrum, a straight or slightly deflexed rostrum about 80% of the length of the first cephalic tooth, and a triangular second cephalic tooth 40% of the length of the first. The short deflexed rostrum of the holotype may be a result of damage, as a slightly smaller, immature male has a straight rostrum equal in length to the first cephalic tooth.

Although urosomites 2 and 3 are rigidly fused to each other, the line of fusion is still apparent in some specimens. The number of distal serrations on the first two coxae increases with increasing size.

REMARKS. *L. grimi* is characterized by low teeth on peraeonites 1–4, peraeonite 1 with two teeth, coxa 1 distally not strongly bifid, and is thus related to *L. pangola* Barnard, 1962 and *L. occlo* Barnard, 1973.

L. pangola and the new species are of similar size and agree in the configuration of the coxae, but differ significantly in sufficient characters to justify separation. In contrast to *L. grimi, L. pangola* has rudimentary teeth on the anterior peraeonites, naked head, peraeon and pleon, epimera 1–2 with weakly convex posterior margins, epimeron 2 lacking facial setae, a short first cephalic tooth, peraeopods 5–7 with relatively short dactyls, the telson cleft less than 50% of its length, and the inner ramus of uropod 1 only 50% as long as the outer ramus.

L. grimi and *L. occlo* differ in that the latter has a body ornamentation consisting of sparse spines rather than dense setae, weakly convex posterior margins of epimera 1–2, a short first cephalic tooth, and a strong cusp at the anterior-ventral angle of the head. Further features which distinguish *L. occlo* are the relative lengths of the antennal peduncles, proportions of the fourth and fifth peduncle articles of antenna 2, short accessory flagellum, weakly cleft lower lip, low spine tooth counts on maxilla 1 palp and maxilliped outer plate, weakly bifid coxa 1, long oblique gnathopod palms, and relatively short, poorly setose uropod 3 rami.

L. grimi bears a strong resemblance to *L. huaco* Barnard, 1973 in characters pertaining to pleon, epimera, mouthparts, coxae and gnathopods. The two species are easily separable, however, by the condition of peraeonites 1–4. *L. huaco* has only a single tooth on peraeonite 1 and none on peraeonites 2–4.

Lepechinella skarphedini sp. nov.
(Figs. 7–9)

MATERIAL EXAMINED. Sta. 7709# 62 1 ♂ 8 mm, 1 ovig. ♀ 10 mm, 1 ♀ 9 mm; Sta. 7709# 72 4 ♂ 7–9 mm, 3 ovig. ♀ 10–11 mm, 4 ♀ 8–9 mm, 1 juv. 4 mm, HOLOTYPE ♂ B.M.(N.H.) reg. no. 1978: 237 [carcase and 3 microscope preparations], 11 PARATYPES 1978: 238; Sta. 7709# 73 14 ♀ 6–10 mm, 6 ovig. ♀ 8–11 mm, 9 ♀ 7–9 mm, 18 juv. 3–6 mm, 2 damaged specimens; Sta. 7709# 85 2 ♂ 8 mm, 1 ♀ 7 mm.

Material from Sta. 7709 # 72 has been deposited in the collections of the Zoology Department of the British Museum (Natural History); all other specimens have been retained at the Institute of Oceanographic Sciences.

ETYMOLOGY. Skarp-Hedin, eldest son of Burnt Njal.

DESCRIPTION. Holotype, male, 9 mm from Sta. 7709 # 72. *Peraeon,* all segments dorsally dentate, teeth 40–50% of height of corresponding segment; peraeonites 1–4 each with one upright tooth; peraeonites 5–7 carinate, teeth acute, posteriorly directed. *Pleon,* each segment dorsally carinate, carinae strongly produced posteriorly. *Epimera,* weakly to moderately convex posteriorly; each with prominent, acute, posterior-distal tooth. *Urosome,* first segment strongly produced dorsally, tooth reaching almost to base of telson; urosomite 3 acutely produced over base of telson. *Body,* rather sparsely setose, finely scabrous.

Head, sparsely setose; rostrum slightly curved, 30% of length of first peduncle article of antenna 1; first cephalic tooth about as long as rostrum; second cephalic tooth irregularly tapering to acute apex, length about 65% of first tooth. *Antenna 1,* about as long as head, peraeon and pleon combined; peduncle 35% of total length, subequal to peduncle articles 1–4 of antenna 2; article 1 60% of length of article 2, both articles bearing setal bundles posteriorly; accessory flagellum 30% of length of first article of primary flagellum, length twice width. *Antenna 2,* 1·4 times length of antenna 1; peduncle articles 3–4 with setal bundles anteriorly, article 5 very slender, 40% longer than articles 1–4 combined. *Upper lip,* asymmetrically rounded. *Mandible,* incisor process blunty dentate; lacina mobilis of left mandible laminar, dentate, that of right mandible bluntly dentate, teeth in two rows; molar triturative; palp as long as body of mandible, article 1, short, 25% of second, article 3 60% of second. *Lower lip,* thick, fleshy, inner lobes broad. *Maxilla 1,* inner plate slender, with two curved plumose setae apically; outer plate with eleven stout dentate spine teeth distally; palp slender, second article long with seven blunt spine teeth on oblique distal margin. *Maxilla 2,* inner plate shorter and much more slender than outer, bearing setae on rounded apex and single stout plumose seta distally on medial margin; outer plate broadly rounded, apically setose. *Maxilliped,* inner plate rather slender; outer plate not broad, bearing six blunt spine teeth medially and five stout spines distally; palp slender, second article elongate, third and fourth articles subequal, unguis of dactyl as long as basal part.

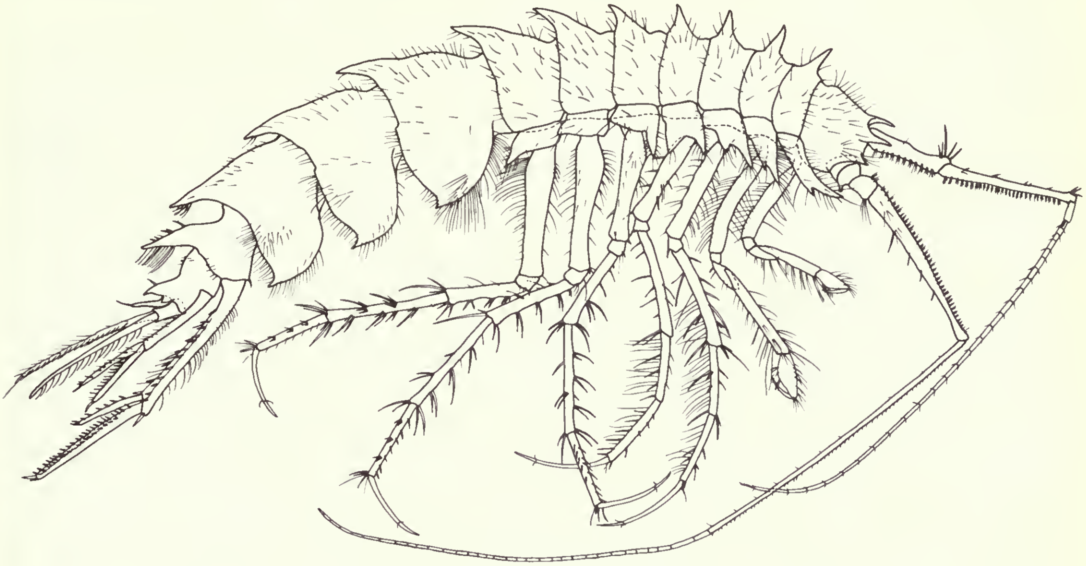

Fig. 7. *Lepechinella skarphedini* sp. nov. Holotype, male, 9 mm.

Gnathopod 1, coxa bifid, anterior lobe longer and broader than posterior, marginally bearing long plumose setae; distal articles rather short and stout; rhomboidal propod about 65% of length of carpus, palm and posterior margin subequal. *Gnathopod 2,* coxa tapering distally, marginally setose, narrowly bifid, posterior lobe small; carpus slender; propod subtriangular, 45% of length of carpus, palm and posterior margin subequal. *Peraeopod 3,* coxa marginally setose, bifid, lobes acute, unequal, anterior the larger; merus and dactyl subequal, longer than carpus and propod. *Peraeopod 4,* coxa marginally setose, symmetrically bifid, lobes acute, shorter than anterior lobe of coxa 3; distal articles similar to those of peraeopod 3. *Peraeopod 5,* coxa with long, acute, setose ventrally directed anterior lobe; basal as long as corresponding article of peraeopods 3–4. *Peraeopod 6,* coxa a parallelogram, posterior-distal angle acute; basal longer than basal of peraeopod 5, equal to peraeopod 7. *Peraeopod 7,* coxa rounded anterior-distally, strongly and acutely produced posterior-distally.

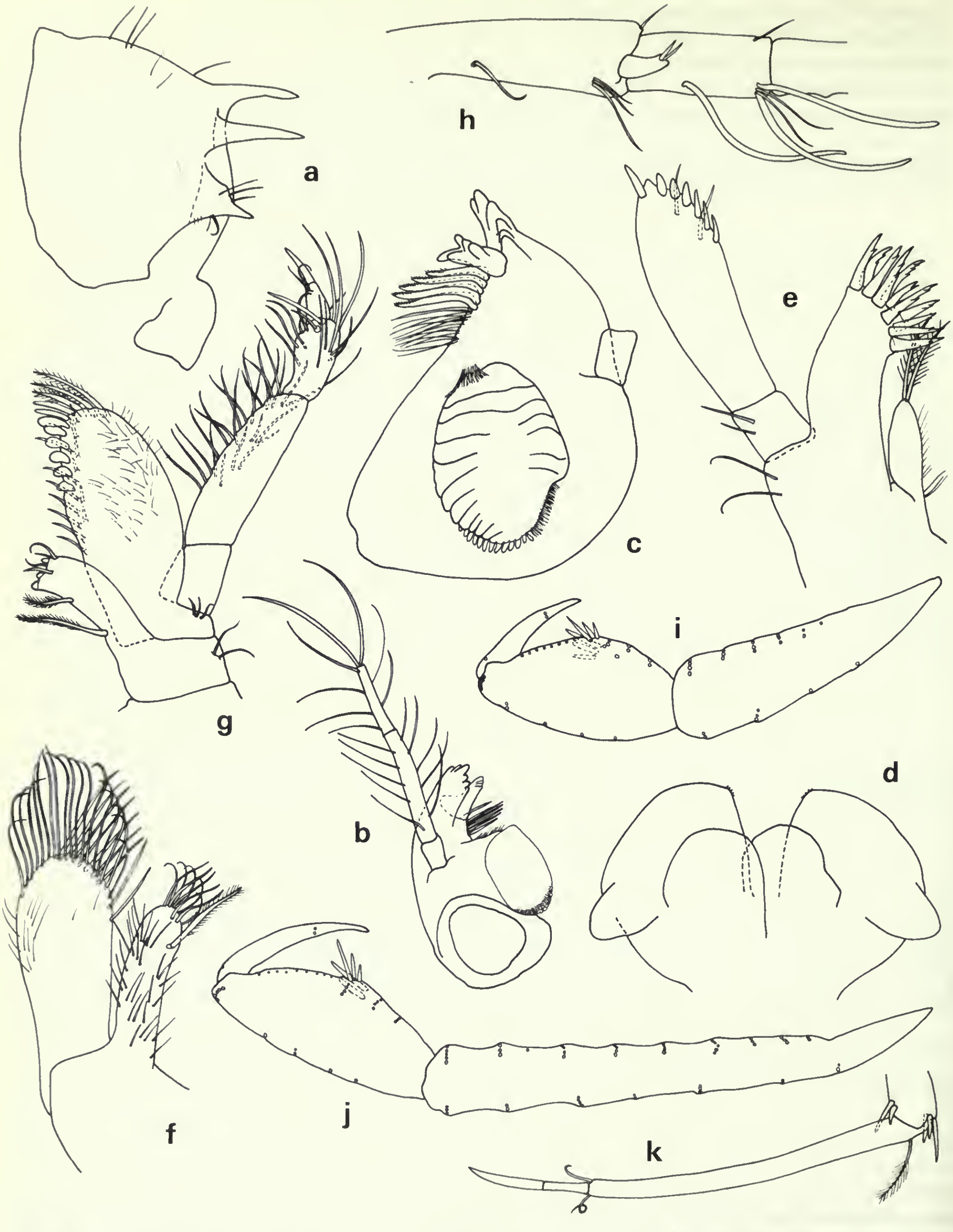

Fig. 8. *Lepechinella skarphedini* sp. nov. Holotype, male, 9 mm. (a) head; (b) left mandible; (c) right mandible, detail; (d) lower lip; (e–f) maxillae 1 & 2; (g) maxilliped; (h) accessory flagellum; (i–j) gnathopods 1 & 2; (k) peraeopod 4, dactyl.

Peraeopods 5–7, merus, propod and dactyl subequal, shorter than carpus.

Uropod 1, strongly spinous; peduncle bilaterally fringed with seta; outer ramus straight, 70% of length of peduncle; inner ramus more slender, 50% of length of outer. *Uropod 2,* short, spinose, not reaching extremity of inner ramus of uropod 1; rami subequal, 75% of length of peduncle. *Uropod 3,* not reaching extremity of uropod 1; peduncle very short, rami subequal, setose, outer with minute second article. *Telson,* setulose, rather narrow, cleft 60% of length, each apex bearing a long stout spine and a seta.

VARIATION. Sexual dimorphism of the kind apparently typical of the genus is found in the dorsal armature, and the setal armature of the antennal peduncles. The dorsal profile of juveniles, females and non-adult males is closer to that of *L. monocuspidata* than is the holotype, as the teeth are shorter, about 30% of the height of the corresponding segment, and less strongly carinate. The rostrum of *L. skarphedini* shows a considerable degree of variation, both in terms of length and shape. The length may be 55–100% of the length of the first cephalic tooth and the rostrum may be gently deflexed as it is in the holotype, straight or upturned. In extreme cases the profile of the head may resemble that figured for *L. monocuspidata* by Barnard (1961, Fig. 68).

REMARKS. *L. skarphedini* is characterized by prominent teeth on peraeonites 1–4, peraeonite 1 with a single tooth, and by the bifid coxa 1.

L. uchu Barnard, 1973 differs from the present species in that coxa 1 of the former is deeply bifid, the emargination between lobes being 40% of the total length of the plate. Coxa 2 is also deeply bifid and has anterior and posterior margins subparallel with the posterior lobe just more than half the length of the anterior lobe. *L. uchu* can also be distinguished by the enlarged outer ramus of uropod 1 which is longer than the peduncle even in juvenile specimens and the reduced inner rami of uropods 1–3 which are respectively 20%, 33% and 80% of the length of the corresponding outer rami. *L. skarphedini* is very similar to *L. monocuspidata* Barnard, 1961 but can be distinguished by a number of quantitative characters. The latter species has coxa 1 indistinctly bifid, coxa 2 not bifid, the posterior-distal teeth of the epimera either absent or very small, the dactyls of peraeopods 3–4 not longer than the corresponding propod, uropod 1 outer ramus distinctly thickened, and uropod 2 very small and barely reaching the distal extremity of the peduncle of uropod 1. Although these differences are mostly of a relatively trivial nature it seems advisable at present to regard the two entities as distinct species. More material from other localities and a greater knowledge of geographical variation may require a closer alignment of *L. skarphedini* and *L. monocuspidata.*

***Lepechinelloides* gen. nov.**

DIAGNOSIS. *Body* with large processes located in dorsal midline, never subdorsally; cuticular spines raised on peg-like projections. *Urosome,* segments 2 and 3 coalesced. *Head,* lacking eyes, rostrum and cephalic teeth. Antenna 1, peduncle articles 2 and 3 subequal. *Mandible,* molar nontriturative; palp of one article. *Lower lip,* inner lobes fleshy, well developed. *Maxilla 1,* palp biarticulate; *Maxilliped,* palp with four articles. *Gnathopod 2,* unguis of dactyl elongate. *Peraeopods 3–4,* carpus elongate. *Uropod 1,* rami immensely long.

TYPE SPECIES. *Lepechinelloides karii* sp. nov.

REMARKS. Non-diverse peraeopods 5–7 place *Lepechinelloides* in the Dexamininae. The absence of rostrum and ocular lobes, and the immensely long uropod 1 are unique within this sub-family. The new genus and some species of *Lepechinella* are closely related, having in common elongate antennae, peraeopod and uropods, strongly developed dorsal teeth, spinous cuticle, and long acuminate coxae. *Lepechinelloides* can be distinguished from *Lepechinella* and *Paralepechinella* by the absence of rostrum and cephalic teeth, and the vestigial mandibular palp of the former. *Atylus* species are rostrate, possess ocular lobes, and

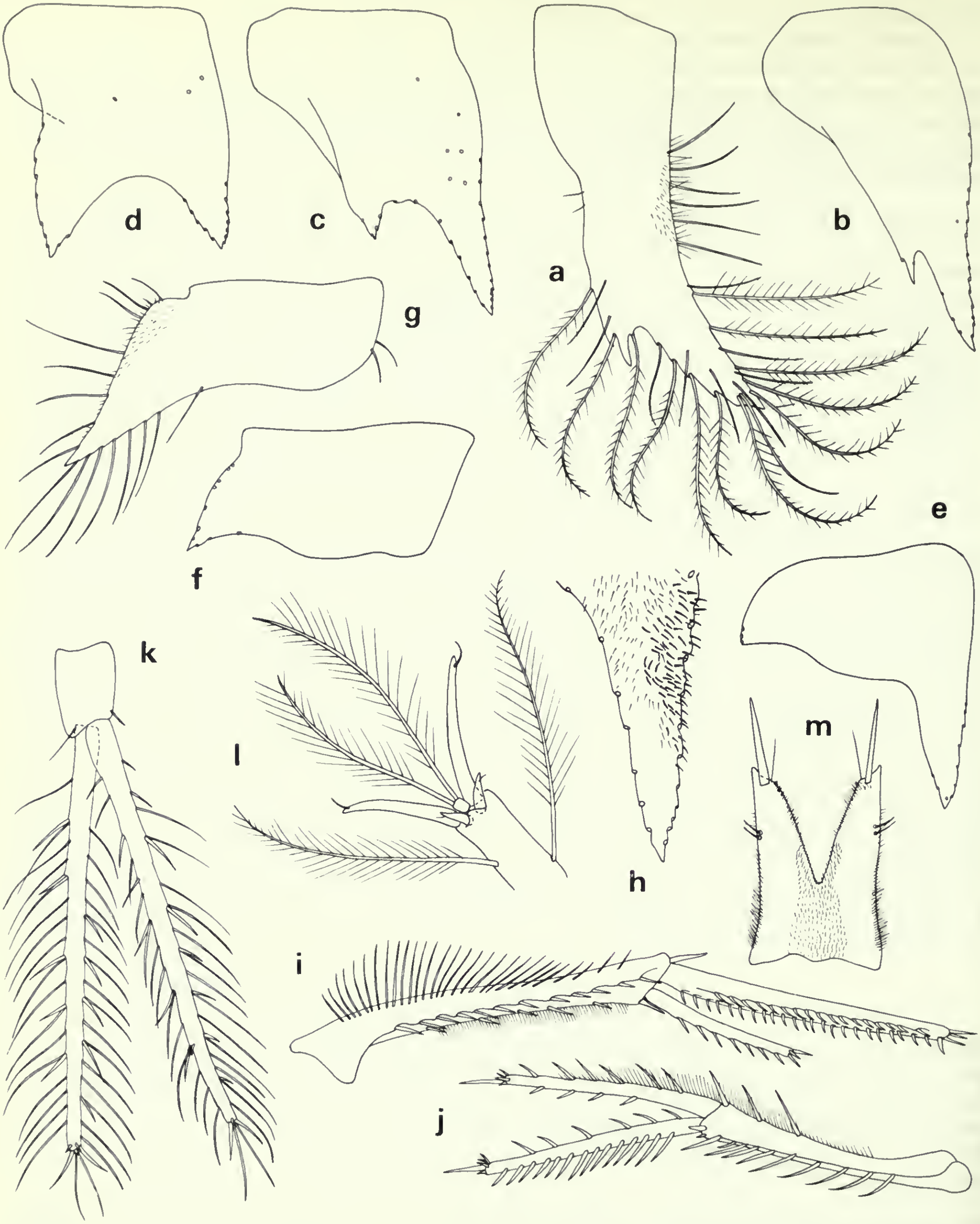

Fig. 9. *Lepechinella skarphedini* sp. nov. Holotype, male, 9 mm. (a–g) coxae 1–7; (h) coxa 3, detail; (i–k) uropods 1–3; (1) uropod 3, detail; (m) telson.

most have lower lips lacking inner lobes and other than uniarticulate mandibular palps. The remaining seven genera of the Dexamininae, *Dexamine, Tritaeta, Dexaminella, Delkarlye* Barnard, 1972, *Paradexamine, Syndexamine* and *Polycheria* are all oculate and all lack even a rudiment of the mandibular palp. In addition, the first six genera have a uniarticulate maxilla 1 palp, and the first four have triarticulate maxilliped palp.

Lepechinelloides karii sp. nov.

(Figs 10–12)

MATERIAL EXAMINED. Sta. 7709 # 62 3♂ 5–7 mm, 3 ♀ 6 mm, 2 juv. 2 mm; Sta. 7709 # 66 1 ♂ damaged, 1 ovig. ♀ 6 mm, 2 ♀ damaged; Sta. 7709 # 72 11 ♂ 6–7 mm, 3 ovig. ♀ 7–8 mm, 13 ♀ 4–8 mm, 7 juv. 3–4 mm, HOLOTYPE ♀ B.M.(N.H.) reg. no. 1978:239 [carcase and 4 microscope preparations], ALLOTYPE ♂ 1978: 240, 8 PARATYPES 1978:241; Sta. 7709 # 73 13 ♂ 4–8 mm, 3 ovig. ♀ 7–8 mm, 14 ♀ 5–8 mm, 11 juv. 2–4 mm; Sta. 7709 # 85 2 ♂ 7–8 mm, 1 ovig. ♀ 7 mm, 2 ♀ 5–7 mm, 1 juv. 4 mm.

Material not registered in the Zoology Department of the British Museum (Natural History) has been retained at the Institute of Oceanographic Sciences.

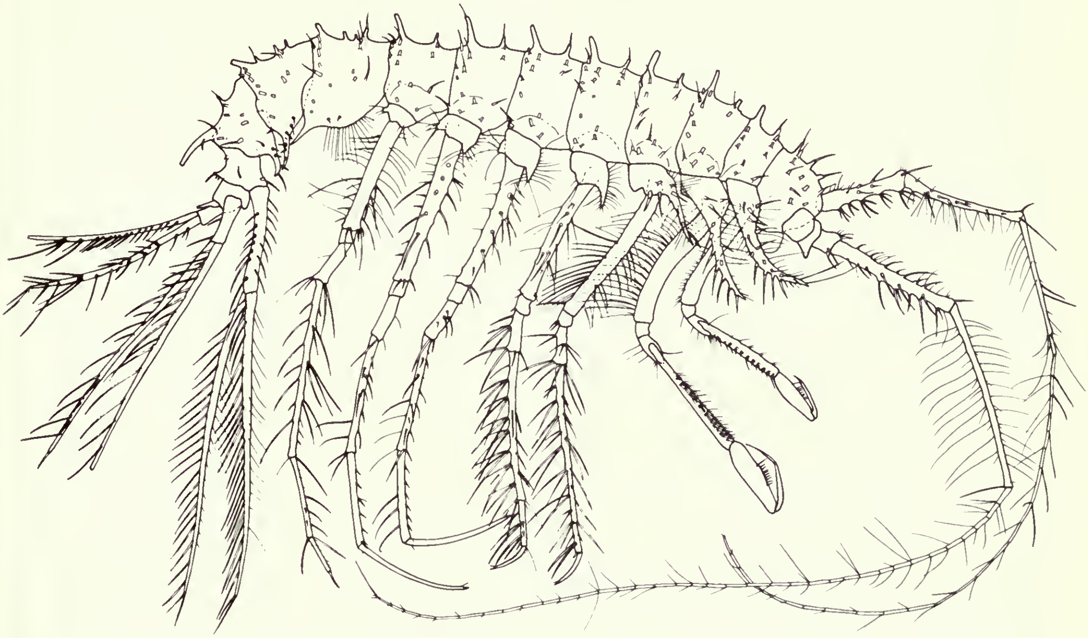

Fig. 10. *Lepechinelloides karii* gen. nov., sp. nov. Holotype, female, 8 mm.

ETYMOLOGY. Kari Solmundarson, husband of Helga, Burnt Njal's daughter.

DESCRIPTION. Holotype, female, 8 mm from Sta. 7709 # 72. *Peraeon,* each segment with upright, columnar projection dorsally close to posterior margin, a smaller peg-like tooth anterior to it, and lateral bosses dorsal to articulation with coxae. *Pleon,* each segment with a columnar projection in the mid-line close to posterior margin, that of pleonite 3 curved posteriorly; pleonites 1 and 2 with three dorsal accessory teeth, pleonite 3 with one. *Epimera,* first broadly rounded with long acute tooth posterior-ventrally; second and third with long curved tooth ventrally. *Urosome,* segments short; first with small, upright tooth posteriorly. *Body,* small peg-like projections each bearing an articulated spine scattered randomly on peraeonites, pleonites, head, coxae, peduncles of antennae and basal articles of peraeopods 3–7.

Head, subglobular, three peg-like projections in dorsal mid-line. *Antenna 1,* about as long as body; peduncle 60% length of filiform flagellum; accessory flagellum a single, elongate article. *Antenna 2,* peduncle rather longer than peduncle of antenna 1; flagellum as long as body. *Upper lip,* shallow, entire. *Mandible,* incisor process broad and laminar, multidentate; lacina mobilis of left mandible laminar, multidentate, of right mandible broad with accessory plate, both cutting edges complexly dentate; molar setose, non-triturative; palp vestigial,

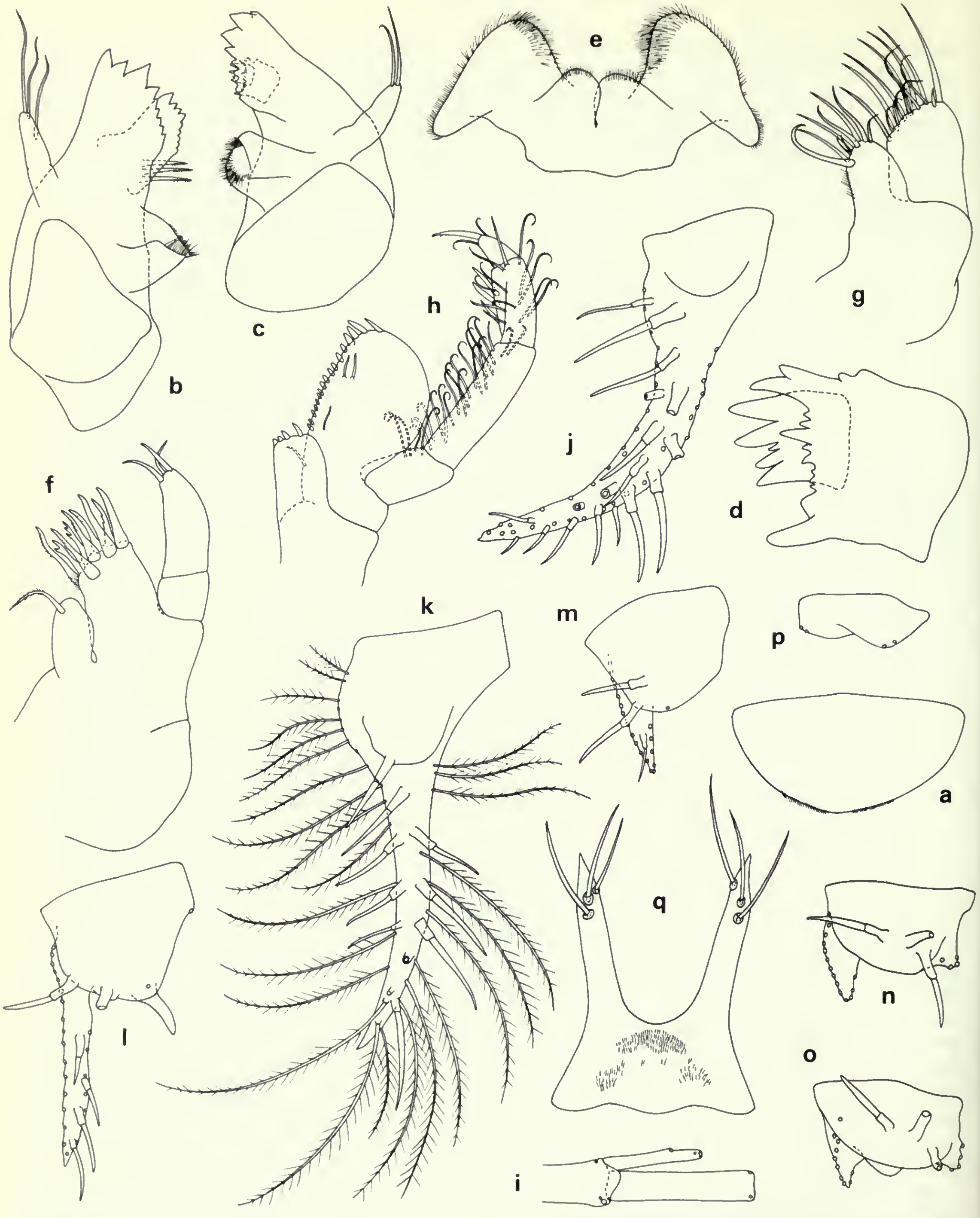

Fig. 11. *Lepechinelloides karii* gen. nov., sp. nov. Holotype, female, 8 mm. (a) upper lip; (b) left mandible; (c) right mandible; (d) right mandible, lacina mobilis; (e) lower lip; (f–g) maxillae 1 & 2; (h) maxilliped; (i) accessory flagellum; (j–p) coxae 1–7; (q) telson.

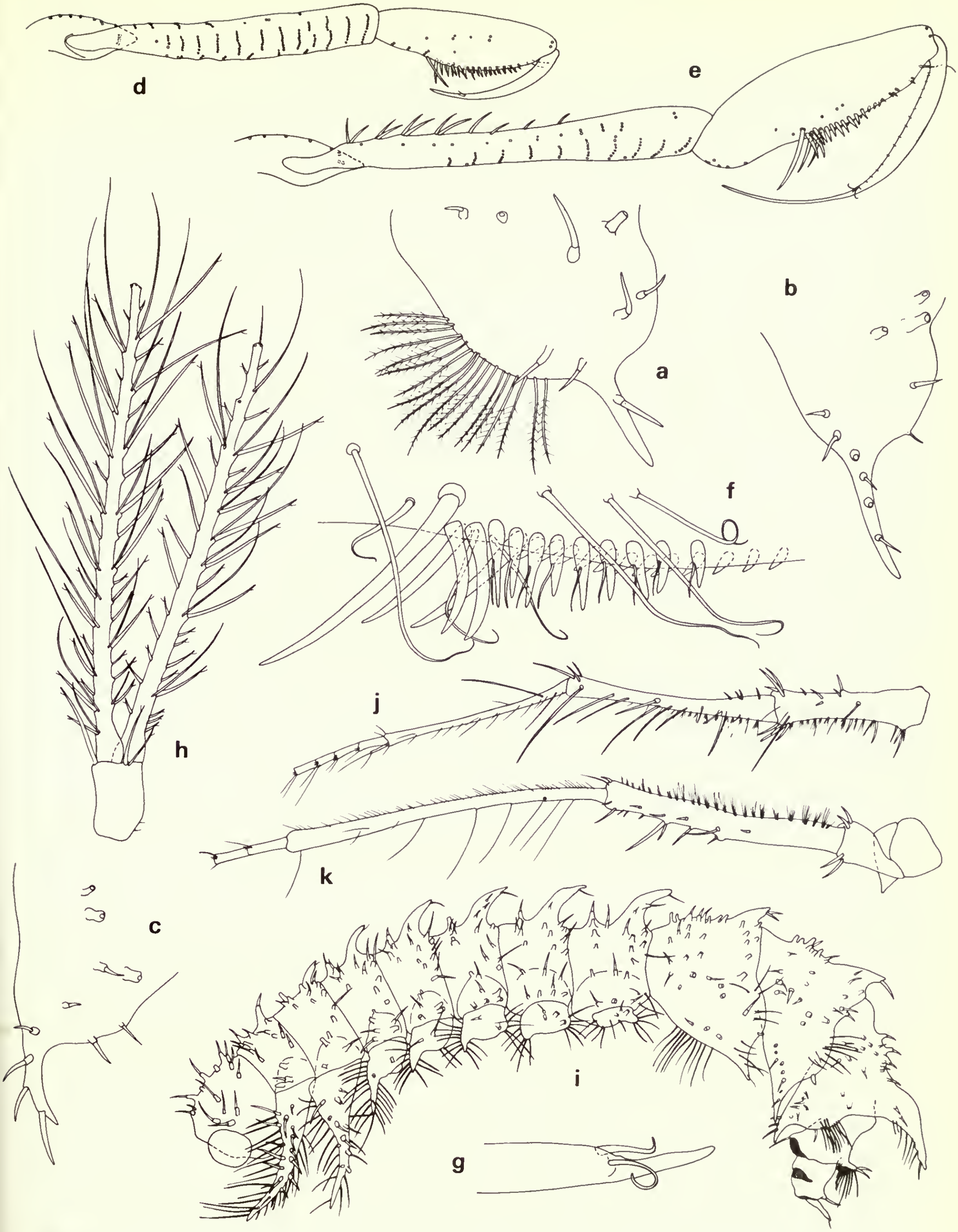

Fig. 12. *Lepechinelloides karii* gen. nov., sp. nov. Holotype, female, 8 mm. (a–c) epimera 1–3; (d–e) gnathopods 1 & 2; (f) gnathopod 2, detail of palm; (g) peraeopod 7, tip of dactyl; (h) uropod 3. Allotype, male 7 mm. (i) body; (j–k) antennae 1 & 2.

with two or three apical setae. *Lower lip,* inner lobes short, broad, outer lobes somewhat gaping. *Maxilla 1,* inner plate small, bearing only an apical seta; outer plate short bearing nine dentate or serrate spine teeth distally; palp poorly developed, second article tapering with three setae distally. *Maxilla 2,* plates short, outer broader than inner. *Maxilliped,* outer plate broadly oval, seventeen small spine teeth along medial margin; palp rather weak, articles linear.

Gnathopod 1, coxa elongate and strongly curved, apically acute, spinous and with basal boss, anterior and posterior margins bearing plumose setae; carpus elongate, slender, armed with ranks of plumose and pectinate setae; propod slender, oval, 60% of length of carpus, palm armed with short spines; dactyl 75% of length of carpus. *Gnathopod 2,* coxa similar to coxa 1 but less strongly curved; carpus slender, elongate, armed with ranks of plumose and pectinate setae; propod larger than that of gnathopod, 1, irregularly oval, 60% of length of carpus, palm spinose, limit marked by strong backwardly directed spine; dactyl as long as propod, curved with slender and enormously elongate unguis. *Peraeopod 3,* coxa thick with an elongate laminar projection anterior-distally bearing spines and setae; remaining articles linear; propod and dactyl short. *Peraeopod 4,* similar to peraeopod 3 except coxal projection shorter. *Peraeopods 5–6,* coxa with short laminar projection anterior-distally, posterior-distal angle subrectangular, bearing setae; merus short; carpus and dactyl subequal; unguis of dactyl very short. *Peraeopod 7,* coxa very small, weakly bilobed; basal shorter than basal of peraeopods 5–6; carpus 1·5 times as long as basal; propod longer than dactyl, both articles combined about 75% of length of carpus.

Uropods, rami slender, elongate, subequal, armed with setae and long slender spines. *Uropod 1,* immensely elongate, barely shorter than peraeopod 7; rami 2·75 times length of peduncle. *Uropod 2,* 80% of length of uropod 1; peduncle short. *Uropod 3,* 50% of length of uropod 1; peduncle very short. Telson, cleft 65%, lobes very slender each with three dorsal, sub-apical spines.

Allotype, male, 7 mm. *Peraeon,* each segment with long, curved posteriorly directed tooth dorsally, main tooth preceded by smaller peg-like projection; main teeth of posterior peraeonites longer and broader than those of anterior segments. *Pleon,* first two segments with several peg-like projections and posterior, triangular dorsal teeth; peraeonite 3 with three small projections and a large, hooked, posteriorly directed tooth. *Urosome,* first segment with upright, setose projection posteriorly; urosomite 3 with small dorsal projection. *Antennae,* subequal, nearly twice as long as body; first and second peduncle articles of antenna 1, and fourth peduncle article of antenna 2 with tufts of sensory setae.

VARIATION. The development of the typical male dorsal armature is more gradual than in species of *Lepechinella.* Immature males show a degree of broadening and hooking of the peraeonal and pleonal teeth prior to the acquisition of sensory setae on the antennal peduncles. The density and length of the cuticular armament varies. It is generally more prominent in larger individuals, with females tending to have fewer and longer pedestals and spines than males. On peraeonites particularly, the pedestal spines tend to occur in transverse bands spreading laterally from the main and accessory mid-dorsal projections.

Discussion

The genus *Lepechinella* was created by Stebbing (1908) for *L. chrysotheras,* and placed in the Paramphithoidae. The junior synonym *Dorbanella,* which Chevreux (1914) included in the Tironidae, was raised to familial status adjacent to the Atylidae by Schellenberg (1924). The family name was changed from Dorbanellidae to Lepechinellidae by Schellenberg (1926) on the realization of the congenericity of the two described species. The allied genus *Paralepechinella,* characterized by an enormously developed mandibular palp, was described by Pirlot (1933). Until Barnard (1970) placed the lepechinellids in the Dexaminidae, the Lepechinellidae was the only gammaridean family confined to bathyal and abyssal depths. Barnard also included the Atylidae, Prophliantidae and Anatylidae in his wider concept of the Dexaminidae. Two evolutionary lines were recognized; a prophliantin line to include *Prophlias, Haustoriopsis, Sphaerophthalmus* and *Guernea,* and a dexaminin line containing the remaining genera.

The well attested similarity between *Atylus* and *Lepechinella* (Schellenberg, 1924; Barnard, 1970, 1973) and the close relation between the latter genus and *Paralepechinella* and *Lepechinelloides* suggest that this group of genera might justify the recognition of an atylin line within the Dexaminidae. The genera of this shallow-water to abyssal group have moderately to strongly modified ocular lobes (except in *Lepechinelloides* where these structures are completely absent), mandibular palps (except two or three aberrant *Atylus*) and biarticulate maxilla 1 palps. The three deep-water genera lack eyes. In contrast, the shallow-water, nestling dexaminins are oculate, show at most weakly modified ocular lobes, have uniarticulate maxilla 1 palps (except *Polycheria*), and lack any trace of mandibular palps.

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A new species of *Hoplophorella* (Acari, Cryptostigmata) from Java

B. W. Parry

Department of Zoology, British Museum (Natural History), Cromwell Road, London, SW7 5BD, England

Introduction

As part of a survey of the world oribatid fauna, Dr Marie Hammer made a collection of soil and litter-dwelling oribatids on Java in 1974. Details of the localities examined and descriptions of the aptychoid species identified were subsequently published (Hammer, 1980), while the euptyctimoid mites were kindly sent to the author for examination. *Phthiracarus anonymum* Grandjean, *Phthiracarus tardus* Forsslund, *Steganacarus striculus* (C. L. Koch), *Rhysotritia ardua* (C. L. Koch) and *Microtritia tropica* Märkel were identified, as well as two specimens of an undescribed species of the genus *Hoplophorella* Berlese, characterized by the presence of spatulate and strongly serrated notogastral setae. A detailed description of this mite is given below. The holotype is deposited in the collections of the Zoological Museum of the University of Copenhagen and the paratype in the British Museum (Natural History), London.

Family **PHTHIRACARIDAE** Perty, 1841

Hoplophorella spatulata sp. nov.

Aspis (Figs 1–3): 180–185 µm long and with a maximum width of 130–140 µm. All the dorsal setae are serrated and procumbent. The lamellar (*la*) and rostral setae (*ro*), approximately 20 µm and 30 µm in length respectively, are rather stout while the interlamellars (*il*) are broadly spatulate and about 30 µm in length. There is a prominent median keel in front of the *il-la* setae and posteriorly the prodorsal integument is raised into a number of longitudinal and transverse ridges. The sensilli, 55–70 µm in length, are membranous and serrated distally, while the basal portion is slender and distinctly cranked. A number of finger-like tracheoles are associated with each bothridium and there is a single pair of short, smooth exobothridial setae (*ex*). The prodorsal integument is coarsely pitted.

Notogaster (Figs 4–6): 300–340 µm in length along a line through c_1–ps_1, and with a greatest depth of 210–220 µm. There are 15 pairs of setae, all of which are short (less than the distance c_1–d_1), spatulate and serrated. The seta c_1 is situated on the posterior margin of the collar and setae c_{2-3} submarginally. The fissures *ip* and *ips* are absent while vestigial f_1 is located just below seta h_1 and f_2 between h_1 and h_2. The notogastral integument is coarsely pitted.

Ano-genital region (Fig. 9): There are three pairs of marginal anal setae (an_{1-3}) and two pairs of adanals (ad_{1-2}) located submarginally. Setae an_{1-3} are all moderately stout, serrated and approximately equal in length. The anterior pair of adanal setae (ad_2) are short and fine while the posterior pair, approximately 55 µm in length, are rather stout and taper to a fine point. Both pairs of adanal setae are weakly serrated. In lateral aspect the paraxial margins of the anal plates are strongly convex and thus rather prominent. There are nine pairs of genital setae (g_{1-9}) and a single pair of aggenitals (*ag*). The latter are located antiaxially in the genital furrows. All the genital setae are short and marginal, the anterior five setae (g_{1-5}) being inserted more closely together than the posterior four (g_{6-9}). There are three pairs of genital papillae, the anterior pair being rather small. The integument of the ano-genital region is coarsely pitted with the exception of the non-setal bearing areas of the anal plates which have no distinct ornamentation.

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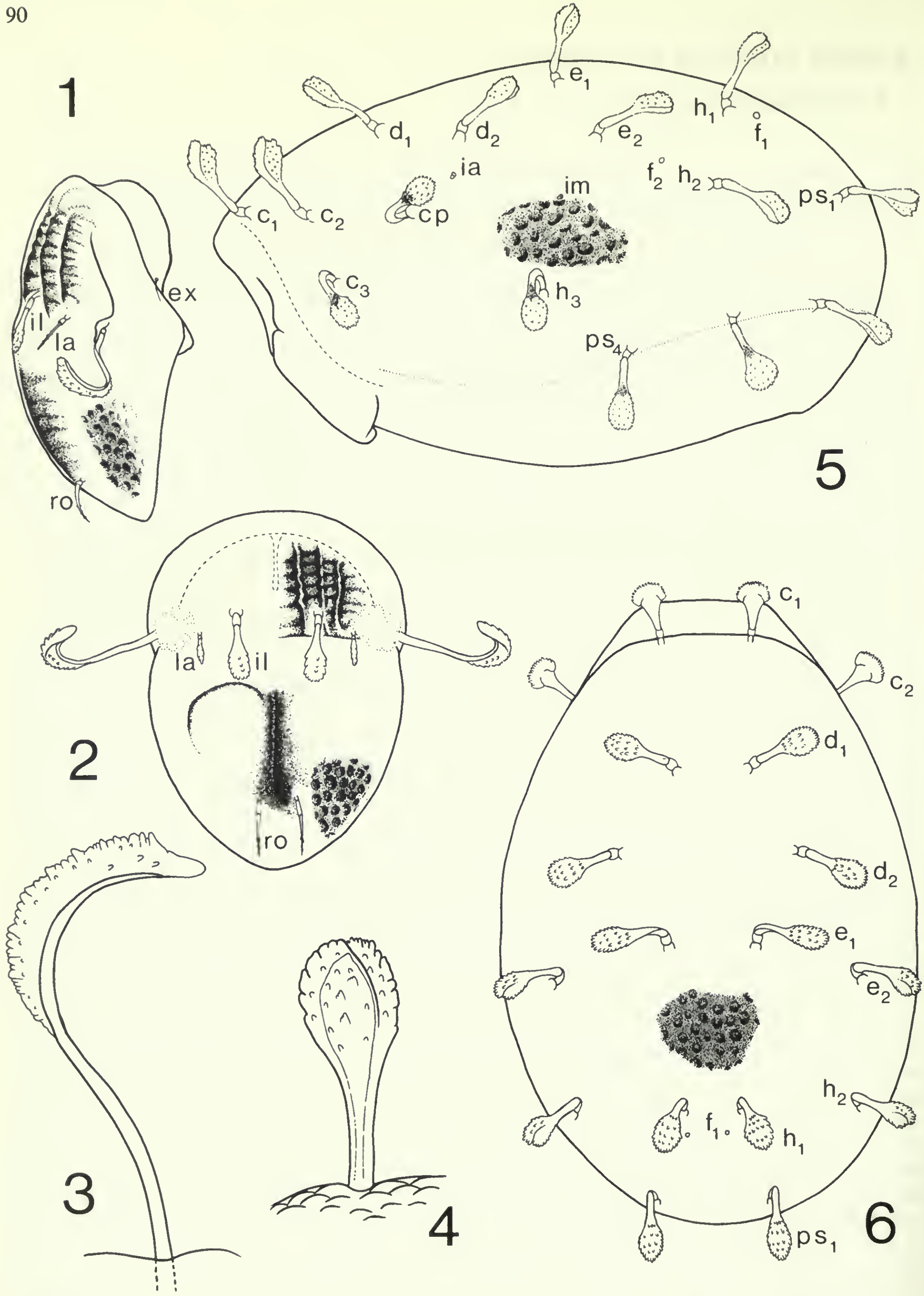
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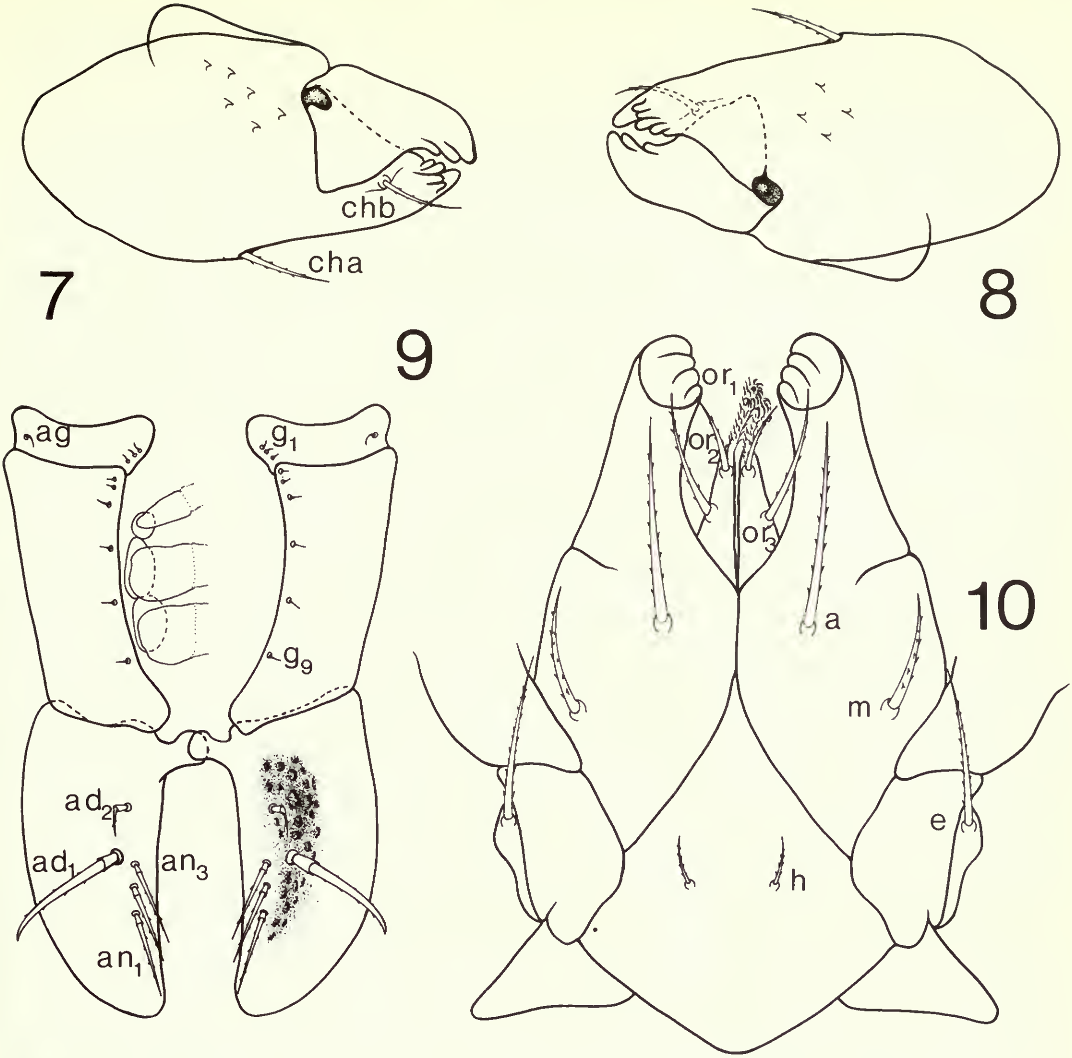
Figs 1–6 *Hoplophorella spatulata:* (1) aspis, lateral; (2) aspsis, dorsal; (3) sensillus; (4) notogastral seta; (5) notogaster, lateral; (6) notogaster, dorsal.

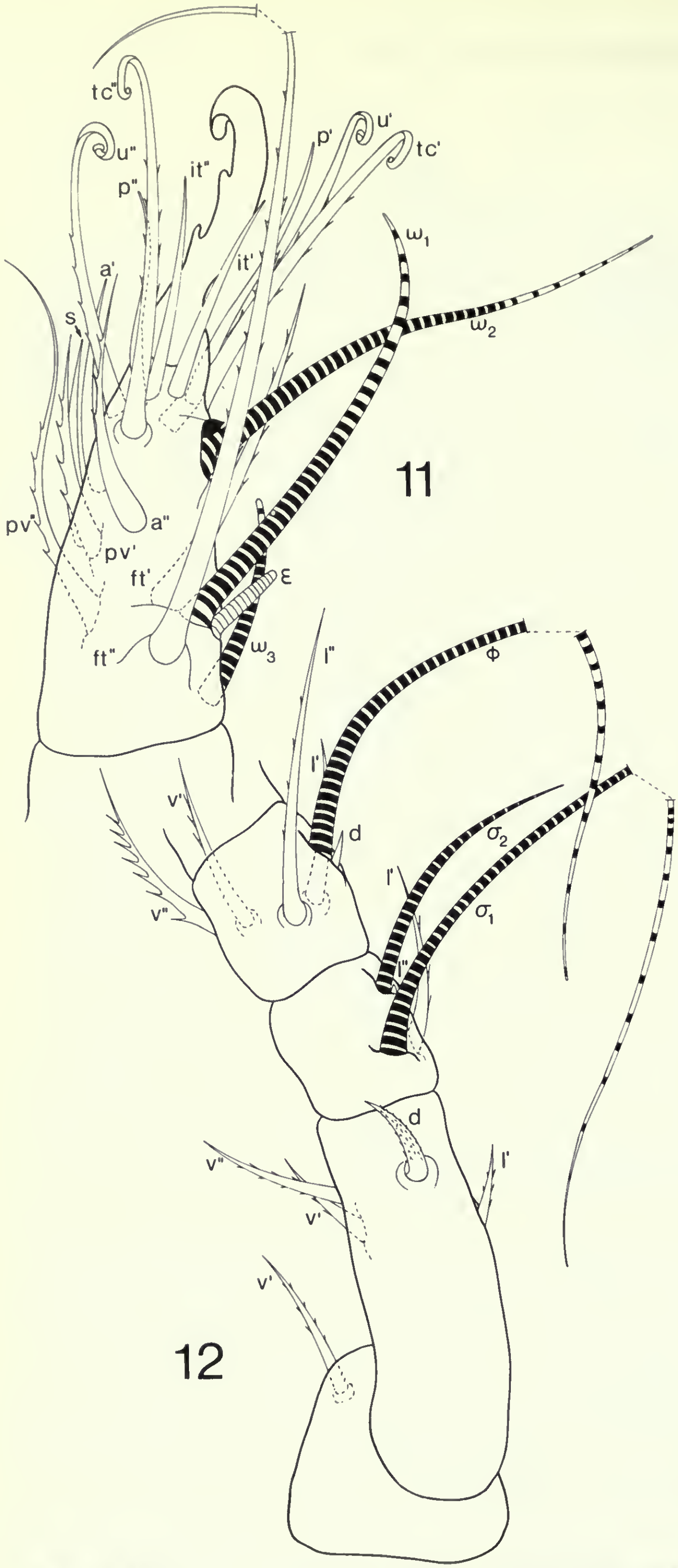


Figs 7–10 *Hoplophorella spatulata:* (7) chelicera, antiaxial; (8) chelicera, paraxial; (9) anogenital region; (10) infracapitulum.

Infracapitulum (Fig. 10): This is typically phthiracaroid in form (see for example, Parry, 1979). There are three pairs of adoral setae, the anterior pair (or_1) being brush-like distally and the posterior two pairs serrated. All the infracapitular setae (*a, m* and *h*) are strongly serrated, the median (*m*) and posterior (*h*) pairs being somewhat shorter than in species of *Phthiracarus* and *Steganacarus*. Laterally there is a single pair of barbed supracoxal setae (*e*).

Chelicerae (Figs 7, 8): The movable digit has three teeth and the fixed digit carries five. There are about six short conical spines on the antiaxial surface of the principal segment and about three sharply pointed spines paraxially. Setae *cha* and *chb* are both serrated, *cha* being somewhat longer than *chb*. The cheliceral integument is finely punctate.

Legs (Figs 11–14): The solenidial and setal formulae for the legs are I (2–1–3) and (1–4–2–5–16–1); II (1–1–2) and (1–3–2–3–12–1); III (1–1–0) and (1–2–1–2–10–1); IV (0–1–0) and (2–1–1–2–10–1). All the solenidia are long and straight. On tarsus I solenidion ω_2 has a small distal coupling seta; its form can only be seen clearly in scanning electron micrographs. On tibia I the dorsal seta coupled with solenidion φ is relatively long and prominent but on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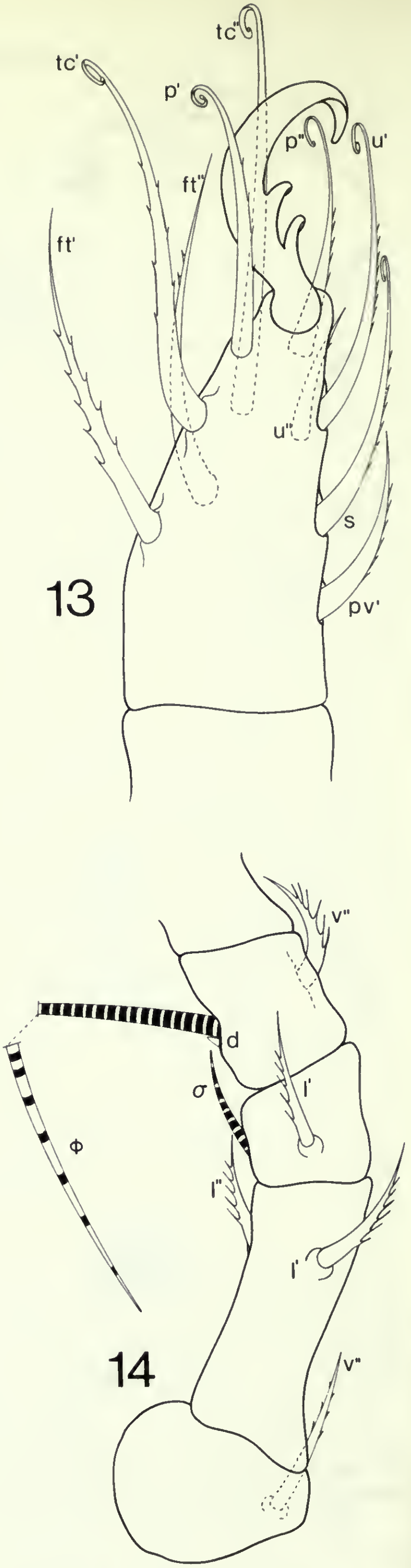
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Figs 11 & 12 *Hoplophorella spatulata,* posterolateral aspect of leg I: (11) tarsus; (12) tibia to trochanter.

Figs 13 & 14 *Hoplophorella spatulata,* anterolateral aspect of leg III: (13) tarsus: (14) tibia to trochanter.

tibiae II–IV it is much shorter. The solenidion σ_2 on genu I is coupled with a reduced posterolateral seta. On all four legs the setal arrangement closely resembles that found in other phthiracaroid genera. Setae (*tc*) and (*u*) on tarsus I and (*tc*), (*u*), (*p*) and *s* on tarsi II–IV are covered with whorls of sharply pointed spicules in the middle third. Such an arrangement of spicules has been observed in two other phthiracaroid genera, namely *Phthiracarus* (Parry, 1979) and *Steganacarus* (Parry, 1978) but the spicules here are rather blunt. Seta *d* on femora I–III is thickened and densely serrated, the serrations being sharply pointed. On tarsi III and IV seta *u''* is short, thick and resembles a eupathidium, while seta *u'* is long, simple and hooked distally (this condition has also been observed in species of *Phthiracarus*).

MATERIAL: Holotype, from moist moss on trunk of *Samanea saman,* Bogor's Botanical Garden, Java, deposited in the collections of the Zoological Museum of the University of Copenhagen. Paratype, BMNH reg. no. 1979.4.6.1, from the above locality. The material was collected by Dr Marie Hammer, 30 January, 1974.

REMARKS: *Holophorella* was proposed by Berlese (1923) as a subgenus of *Phthiracarus,* with *Phthiracarus* (*Hoploph.*) *cucullatus* (Ewing) as type. The following diagnosis was later published by Jacot (1933) who regarded *Hoplophorella* as a separate genus: 'The chitin is usually areolated or otherwise sculptured, and the anal covers are strongly convex, thus protruding beyond the ventral plate and [the] line of genital covers. The anal covers bear only three, subequally spaced bristles on median edge.' In relation to the first two characters, *Hoplophorella* has obvious affinities with *Steganacarus* and *Tropacarus* and the only diagnostic feature of the genus appears to be the chaetotactic pattern of the anal setae. Van der Hammen (1959) suggested that the presence of a notogastral hood could provide an alternative basis for separating *Hoplophorella* from other Phthiracaridae, but since this character is evident in less than half the known species of the genus, and while a hood closely approaching the condition in *Hoplophorella* is found in species of *Steganacarus* and *Tropacarus,* this cannot be diagnostic for *Hoplophorella.* Moreover, the results of Sheals' (1969) numerical analysis of the Phthiracaroidea confirm that *Hoplophorella* is neither a very 'natural' nor a distinctive genus. The leg chaetotaxy, at least in *H. spatulata,* closely resembles the condition found in the rest of the Phthiracaroidea (see Parry, 1979) but unfortunately there is no information available on the pattern and numbers of setae in other described species of *Hoplophorella.*

It would appear that *H. spatulata* bears a somewhat unusual form of notogastral seta for, although spatulate setae have been described in other species of the genus (for example, *H. cucullata*) these are smooth and not densely serrated as in the species from Java. Moreover, the nature of the prodorsal integument presents another unusual feature for, in addition to a number of longitudinal ridges, *H. spatulata* possesses a series of transverse ridges, thus giving a 'lattice' effect to the integument posterior to setae *il-la.*

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On a new species of *Rousettus* Gray, 1821, from Sumatra and Borneo (Mammalia: Megachiroptera)

W. Bergmans

Instituut voor Taxonomische Zoölogie, Plantage Kerklaan 36, 1018 CZ Amsterdam, The Netherlands

J. E. Hill

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD, England

Synopsis

Rousettus spinalatus n.sp. is described, based on an adult female and a juvenile male from the vicinity of Medan, Sumatra. It has also been found at Niah, Sarawak, Borneo. Its nearest living relative, with which it is at least partly sympatric, is *Rousettus amplexicaudatus* (Geoffroy Saint-Hilaire, 1810). The most obvious external characters by which *spinalatus* differs from this and other possible relatives are the high insertion of the endopatagium on the back next to the spinal line, and the subsequent absence of a true longitudinal dorsal band of fur between both endopatagial insertions. The new species differs further from *amplexicaudatus* in the shape and relative size of certain teeth. Earlier records of *Rousettus amplexicaudatus* from Sumatra are reviewed and a third species, *R. leschenaulti* (Desmarest, 1820), is recorded from that island for the first time.

Introduction

Recently, two fruit bats of the genus *Rousettus* Gray, 1821, were collected in northern Sumatra and were sent to the Naturhistorisches Museum in Vienna (NMW). The Curator of Mammals, Dr K. Bauer, identified them as related to *Rousettus amplexicaudatus* (Geoffroy Saint-Hilaire, 1810) but doubted this determination on the ground of the extremely high wing insertion and sent them to one of us (Bergmans) for further study.

Some years ago Hill had received a similar specimen from Sarawak, Borneo. At the time he was reluctant to attach taxonomic significance to the peculiar condition of the wing insertion, considering that even if the specimen was not an aberrant example of *amplexicaudatus* it was, as a single subadult, inadequate as a basis for a new taxon.

New and detailed study of the Sumatran specimens and of the example from Borneo lead us to believe that they represent a hitherto unnamed species of the genus *Rousettus*, for which reason it is described below. Colours have been compared with the colour plates of Ostwald (1939) and translated into Ridgway colours with the tables of Zimmermann (1952). All measurements are in mm. The illustrations are by the first author.

Rousettus spinalatus n.sp.

Rousettus amplexicaudatus, Harrison, 1967: 229 (partim: the ♀ specimen caught 6 November in Niah Great Cave).

HOLOTYPE. Adult female, skin and skull, collected in December 1977 in northern Sumatra (either in or near Medan, or in or near Prapat), by natives for Dr Kern (NMW 24112).

PARATYPE. Juvenile male in alcohol, young of the holotype; all data as for holotype (NMW 24113).

REFERRED MATERIAL. Subadult female, skin and skull, collected 6 November, 1965 at Niah Great Cave, Sarawak, Borneo (3° 52′ N, 113° 44′ E) by T. Harrisson (BM(NH) 75.589).

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DESCRIPTION OF HOLOTYPE (remarks on paratype and on subadult from Sarawak stated as such). A rather small pteropine bat with all the characters typical of the genus *Rousettus* Gray, 1821, as diagnosed by Andersen, 1912, except for its high wing insertion. If subgenera are to be recognized within this genus, a member of the nominate subgenus with moderately deflected braincase, relatively broad cheek teeth, wings inserted at first toe, and a distinct antitragal lobe.

Head. Rostral part of head rather conical, sparsely furred with extremely short very dark brown (about Bone-Brown) hairs, with about 15 small warts bearing one longer hair each at either side between nostril, eye and upper lip, 10 to 15 such warts at either side of chin on lower lip, and about 6 at either side on area under eye behind mouth corner. Nostrils separated by a vertical cleft, slightly protruding, directed forward and outward. Chin pad widely V-shaped, with shallow groove in median plane and notched at its proximal point, and with a short (about 2 mm in paratype) and narrow offshoot at each side along lower lip. Both upper and lower lips rather thick, each with a single row of very small papillae on posterior half of inner margin. Tongue with field of toothed papillae on anterior part. Back of head rather domed. Ears moderately long, rather broad at bases and gradually narrowing to an obtuse point; margins thickened at bases. Antitragal lobe quite distinct, thick. Ears naked but for lower posterior part of outer surface; skin of conch dark brown.

Wings and tail membrane. Insertion of endopatagium (studied initially in the paratype because of its preservation in alcohol) along dorsal side of upper arm to a point just dorsal of axilla; from there in a weak curve backward, approximately following distal margin of scapula, toward spinal line, which is reached at the level of caudal point of scapula; following spinal line until level of the proximal part of the leg, from there further along dorsal side of the proximal part of the leg and shifting to outer side of the distal part of the leg, onto inside of proximal end of first phalanx of first toe. The wing is relatively short and broad, as is usual in *Rousettus.* Dorsally, the tail membrane or uropatagium seems a mere extension of the dorsal part of the endopatagium. It is also inserted along the dorsal side of the proximal part of the leg, along the same commissure as the endopatagium, and further along the inner side of the distal part of the leg and along the spinal line, to a point about halfway along the external tail, forming a pocket above the upper part of each leg. As a consequence, when viewed from the dorsal side, the legs seem to pierce through the membrane at the knees and the upper parts are hidden. From the tail, which is free for its last 4 mm in the paratype, the uropatagial margin runs almost straight towards the calcar, which has a length of 6·5 mm in the holotype, and from this to the inner side of the foot, slightly below the ankle. Wings and tail membrane dark brown; the propatagium, parts of the endopatagium (near the forearm and near the body), and the uropatagium except for a caudal zone are more transparent than the remaining parts of the membranes.

Fur. Interocular area, crown and sides of head to a line from angle of mouth to the base of the ear sparsely furred, the hairs short (up to 4 mm in length), dark brown (about Bone-Brown), somewhat longer on back of head. Nape with very few, long dark hairs (up to 10 mm in length) of the same colour. Lower cheeks and sides of chin and throat with somewhat longer, somewhat less sparse brownish white (near Light Cinnamon-Drab) hairs. Centre of chin and throat almost naked. Anterior part of back between shoulders naked, bordered laterally and posteriorly by a short mantle (total width up to 15 mm) consisting of a narrow band (4–5 mm) of brownish white, near Light Cinnamon-Drab hairs of up to 5 mm in length (some with dark brown tips), a zone of shorter dark brown, near Bone-Brown hairs with brownish white bases, and a zone of very short dark brown hairs. The subadult from Sarawak has a similar triangular naked patch between the shoulders, margined laterally by the rather long, brownish white hairs of the mantle, which towards the rear become shorter and darker brown to margin the anterior edge of the uropatagium over the back. The juvenile paratype has a relatively small triangular naked patch; the long hair on the back of its head extends further backward than in the holotype, and the sides of the neck are also furred. In the holotype there is a mid-dorsal, bald interruption of this mantle of about 5·5 mm width. In the juvenile paratype and in the subadult from Sarawak there is no such interruption: here, the

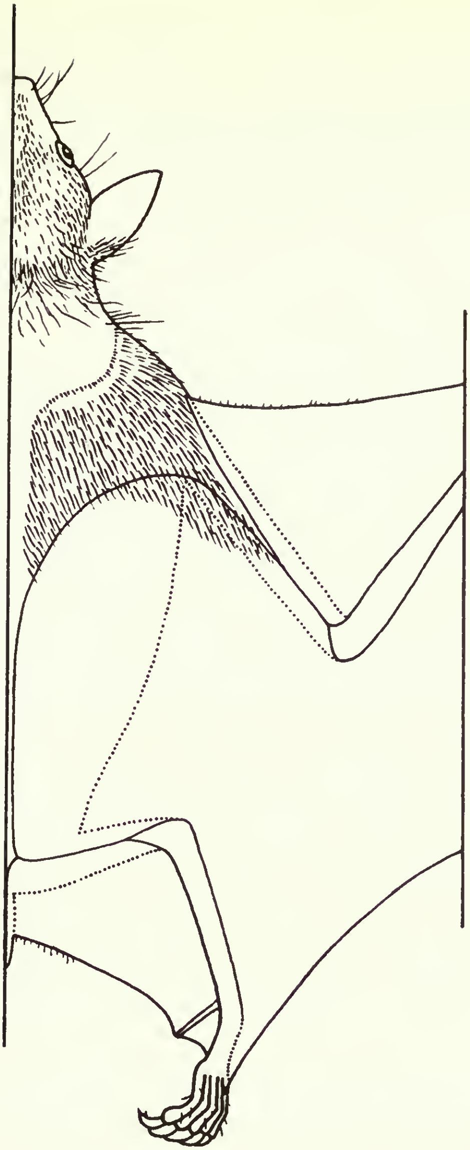

Fig. 1 Diagram of insertion of endopatagium and of dorsal fur distribution in holotype specimen of *Rousettus spinalatus* n. sp. (NMW 24112).

mantle ends, caudally, in a point on the vertebral line. Along the upper arms the mantle continues in a narrow stretch to a point at about 21 mm from the elbow. The lateral borders of the mantle coincide with the insertions of the propatagium, the caudal border with the anterior insertion of the endopatagium. There is a very narrow zone of skin in between the longitudinal insertions of the endopatagium, about 2 mm wide in the dried skin of the holotype and in the subadult from Sarawak, with very few, apparently deciduous, short hairs scattered over the first two thirds of the length of the back. These hairs are very sparse in the holotype and in the subadult from Sarawak but more numerous in the paratype. The dorsal fur pattern is shown in Fig. 1.

Dorsal sides of uropatagium, tibia and toes with sparsely scattered hairs in paratype and in the subadult from Sawarak but almost naked in holotype. Chin and throat sparsely haired with Light Cinamon-Drab hairs on the sides and about naked in the centre. Chest and belly with relatively dense but rather short Drab fur, slightly Tawny Olive in the centre, and darkening towards sides and lower belly. The back under the endopatagium and part of the adjoining sides of the body furred with fairly long (5–8 mm), slightly wavy hairs which are bi-coloured to give the effect of irregular, roughly transverse stripes, alternating dark and light brown and on the average 1 mm wide; this pattern is less obvious in the subadult from Sarawak. Ventral side of upper arm and proximal third of forearm thinly furred with Drab hairs. Proximal half of propatagium with sparse, thin, whitish to Tawny Olive hairs about 5 mm in length; ventral side of endopatagium and small area of mesopatagium near the elbow with similar fur; a few sparse hairs on mesopatagium along distal end of forearm. Ventral side of legs naked, of toes with incidental hairs; the ventral side of tail and surrounding uropatagium with a sparse scattering of thin hairs.

Skull (Figs 2–5). Premaxillae slender, in contact but not co-ossified anteriorly; dorsal profile of rostrum nearly a straight line, very slightly concave through weak upward curve of anterior tip of nasals and somewhat bulging frontal region; posterior part of dorsal surface of rostrum and frontal region with shallow longitudinal median groove, the area between postorbital processes flattened. Temporal ridges separate anteriorly (about 3 mm apart in holotype), uniting at a point about 5 mm from the supra-occipital ridge. Rostrum relatively short, its lower part broad anteriorly. Interorbital constriction similar in width to postorbital constriction; braincase highly domed, and distinctly deflected from cranial axis (direction of alveolar line indicated in Fig. 2). Zygomatic arches slender, their greatest depth 1·3 mm in both holotype and subadult from Sarawak. Relative size of tympanic bullae as in other members of the genus; foramen magnum essentially hexagonal, slightly higher (5·5 mm) than wide (5 mm) in the holotype but slightly wider (5·3 mm) than high (5·1 mm) in the subadult from Sarawak. Mandible slender, relatively broad anteriorly (Fig. 5), with relatively high coronoid process (Fig. 3).

*Teeth** (Figs 2–5) Upper incisors small, the outer tooth (I^2) somewhat larger than the inner tooth (I^1), curved posteriorly and inwardly; I^1–I^1 about as great as width of I^1; I^1 and I^2 almost touching; I^2 separated from canine by a narrow diastema (I^2–C about 1 mm). Upper canine rather short (reconstructed height from cingulum in holotype about 3·4 mm, its height from cingulum in subadult from Sawarak 3·5 mm); basal outline ovoid, the anterior part the widest; a very shallow vertical antero-internal groove; labial face evenly rounded; orientation of lingual slope about equally inward and backward; a narrow but distinct and nearly horizontal lingual shelf; narrow, weakly concave posterior face. Anterior upper premolar (P^1) small, about the bulk of I^2 or slightly heavier. Second upper premolar (P^3) short and narrow, its base obliquely oval in outline; rather sharp antero-external keel; labial face relatively flat; distinct postero-external ridge; antero-internal and postero-internal slopes slightly concave, separated by a ridge-like commissure from tip to cingulum; no lingual shelf (a trace of this in the left P^3 of the holotype). Third upper premolar (P^4) low, its base obliquely rectangular in outline but with greatest width in posterior half; prominent narrow outer ridge with higher anterior cusp; inner ridge short, with lower antero-internal cusp which has a trace of a weak commissure; outer and inner cusps worn in holotype, rather blunt in paratype and in the subadult from Sarawak; postero-external corner differentiated, posteriorly, by a weak inward curve; low postero-internal lingual shelf. First upper molar (M^1) low, rectangular but for a somewhat protruding antero-internal corner; outer ridge narrow, prominent but low, with weak cusp; inner ridge low, with a small cusp (worn in holotype, and not yet erupted in paratype and low in the subadult from Sarawak). Second upper molar (M^2) low, more or less rectangular, anterior width the greatest; outer ridge weak, with trace of cusp; inner ridge and cusp hardly indicated; posterior side 0·3 mm in front of insertion of the lower margin of anterior zygomatic arch. Lower incisors small, the outer (I_2) slightly longer than the inner (I_1), both weakly bifid in the holotype, quite clearly so in the subadult from Sarawak. Lower canine short (reconstructed height from cingulum in holotype about 2·2 mm, its height from cingulum in subadult from Sarawak 2·4 mm); essentially pointing slightly forward and outward, but tip recurving; roughly divisible into a vertically rather straight and horizontally rounded antero-external face and a vertically concave and horizontally rounded postero-internal face, separated labially by an obtuse ridge and lingually by a more distinct but still weak keel; lower part of postero-internal slope almost horizontal, forming an ill-defined and narrow posterior shelf. Anterior lower premolar (P_1) low, squarish, rather small; labial face weakly rounded, lingual face a broad curve; weak but distinct outer ridge and cusp; lingual shelf a weak inward slope. Second lower premolar (P_3) rather high (about 1·8 mm from cingulum), narrow, elongated; pointing slightly forward and outward; anterior keel weak but distinct; labial face rather flat, except anteriorly; antero-internal face rounded; postero-internal face an even slope, well-defined, slightly concave, gradually passing into a narrow, weakly sloping 'shelf'. Third lower premolar (P_4) low, rounded anteriorly and widening into a rectangular posterior part; blunt outer and similar, somewhat lower inner ridge, both running from single medio-anterior cusp; no posterior ledge. First lower molar (M_1) low, long, generally rectangular but slightly wider posteriorly; blunt anterior, labial and lingual ridges; no posterior ledge; surface concave. Second lower molar (M_2) similar to M_1, but shorter, lower and at its widest anteriorly. Third lower molar (M_3) yet smaller and lower, with blunt ridges on all sides and a concave surface.

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*Designation of teeth after Andersen (1912).

Palatal ridges (Fig. 4). Formula 3 + 4 + 1 (division of the 4th ridge narrow, possibly anomalous; see Andersen, 1912 : 19); 6th to 8th ridges serrated. The 1st ridge runs between the posterior halves of C^1–C^1, with a weak backward curve in the middle. The 2nd extends between the anterior halves of P^3–P^3, with a slight forward curve. The 3rd starts at the anterior halves of P^4–P^4 and curves forward to a line joining the posterior halves of P^3–P^3. The 4th begins just behind the antero-internal corners of M^1–M^1 and slants forward to a line joining the centres of P^4–P^4. The 5th starts at the antero-internal corners of M^2–M^2 and reaches the level of the anterior halves of M^1. The 6th begins just behind M^2–M^2 and remains between these teeth. The 7th runs from a point just anterior to the middle of the lateral postdental palatal margin and remains just behind M^2–M^2. The 8th ridge parallels the posterior margin of the postdental palate, increasing its distance only in the centre, where it points forward.

MEASUREMENTS OF THE HOLOTYPE AND (IN PARENTHESES) OF THE SUBADULT FROM SARAWAK. Collector's measurements of holotype: total length 105; forearm lengths 79 and 82·5; ear 17·4.

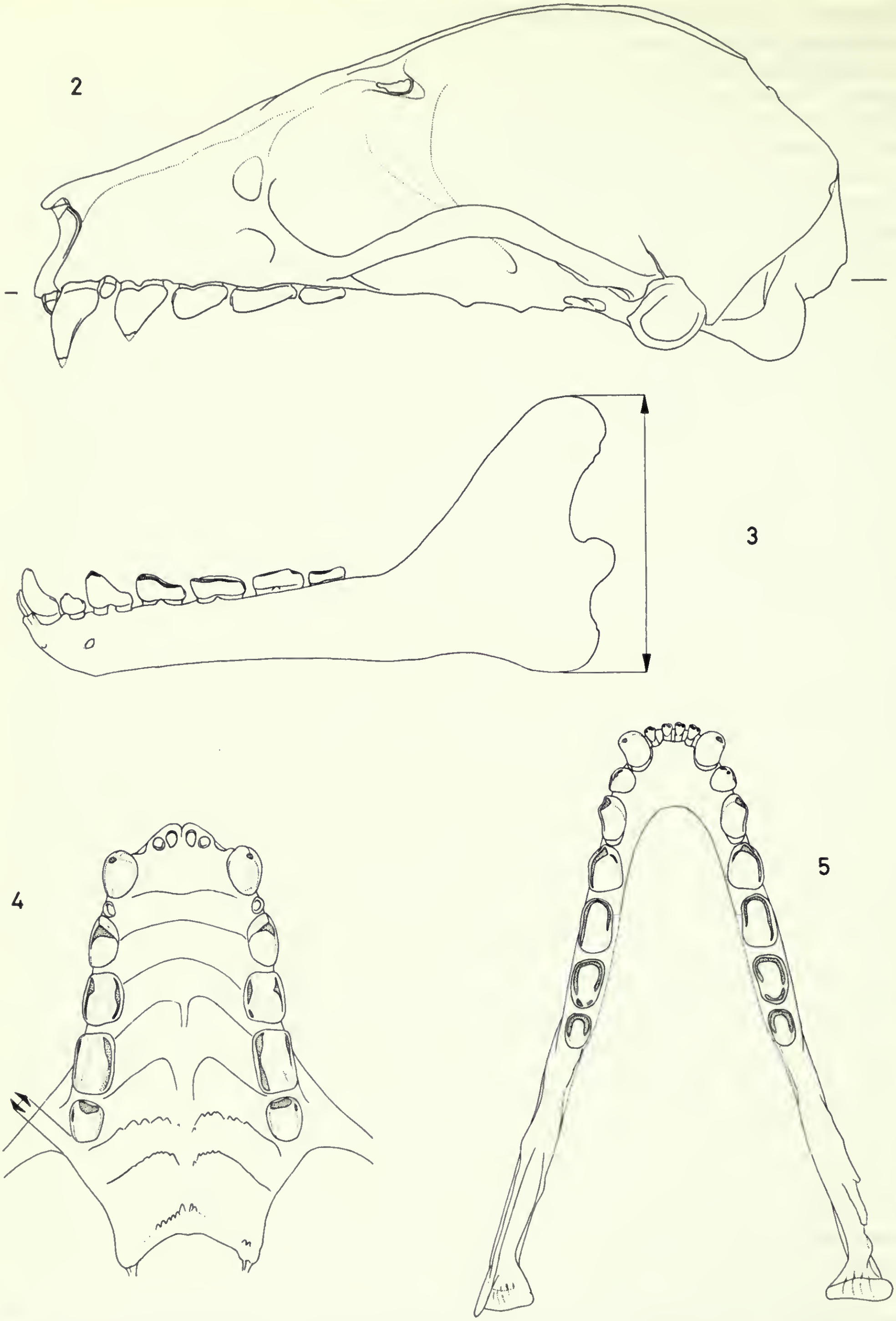
Measurements of the holotype were taken by Bergmans, of the subadult from Sarawak by Hill.

Body: tibia about 31·5 (27·5); foot with claw about 17 (17); forearm length (left) 80·6 ((right) 74·8); 1st digit with claw 25·5 (26·0); 2nd digit, metacarpal 32·3 (29·9), 1st phalanx 6·5 (7·5), 2nd phalanx 4·2 (4·7); 3rd digit, metacarpal 48·3 (43·2), 1st phalanx 30·6 (28·1), 2nd phalanx 41·0 (36·5); 4th digit, metacarpal 47·6 (41·8), 1st phalanx 23·2 (22·3), 2nd phalanx 26·5 (24·7); 5th digit, metacarpal 46·4 (42·2) 1st phalanx 21·6 (20·2), 2nd phalanx 23·5 (23·0); length of second phalanx always measured from end to end when unstretched.

Skull: greatest length 35·1 (33·2), condylobasal length 33·2 (31·0), rostrum length (front of orbit to prosthion) 12·1 (11·4), rostrum length (front of orbit to tip of nasals) 11·0 (10·3), palatal length 17·7 (16·5), cranium width 14·6 (14·2), interorbital width 7·4 (7·4), postorbital width 7·5 (8·5), zygomatic width 20·9 (-), mandibular length 26·5 (24·2), mandibular height (greatest height when mandibulum on a horizontal plane) 11·5 (-).

Teeth: width over C^1–C^1 6·7 (6·5), width between C^1–C^1 3·8 (3·8), length C^1–M^2 (cingula) 12·8 (12·4), width over M^2–M^2 (cingula) 9·9 (10·2), length C_1–M_3 (cingula) 14·1 (13·6). P^3 2·2 × 1·2 (2·1 × 1·4), P^4 2·3 × 1·8 (2·3 × 2·0), M^1 2·8 × 1·8 (2·9 × 2·1), M^2 1·9 × 1·5 (2·0 × 1·8), P_3 2·0 × 1·1 (2·0 × 1·3), P_4 2·2 × 1·5 (2·2 × 1·6), M_1 2·4 × 1·5 (2·5 × 1·7), M_2 2·2 × 1·4 (2·3 × 1·6), M_3 1·7 × 1·1 (1·8 × 1·3).

ETYMOLOGY. The name *spinalatus* has been derived from the Latin words *spina* (= spine) and



Figs 2–5 Skull and dentition of holotype specimen of *Rousettus spinalatus* n.sp. (NMW 24112). (2) Left aspect of skull; alveolar line indicated. (3) Left side of mandible; height indicated. (4) Ventral view of upper dentition and palatal ridges; shortest distance between M^2 and palate margin indicated. (5) Dorsal view of mandible with lower dentition. In the figs 3–5 worn areas on the teeth have been stippled.

ala (= wing) and refers to the insertion of the endopatagium along the spinal line, a unique condition within the genus *Rousettus*.

DISTRIBUTION. *Rousettus spinalatus* is known from the type locality (near Medan or Prapat, Northern Sumatra), and from Niah Great Cave, Sarawak, Borneo.

BIOLOGY. The juvenile paratype has a forearm length of 54·0 mm and was in the process of shedding its milk dentition. It still has its i^1, i^2, c^1 (just behind the emerging tip of C^1), all narrow cylindrical spicules with recurved tips, i^2 somewhat bulkier than i^1, and p_1 or p_2, a slightly heavier tooth in between the tips of P_1 and P_3. The tips of C^1, P^3 and outer ridges of M^1 and M^2 have emerged, and also a large part of I_1, with the tips of I_2, C_1, P_1, P_3, and P_4. Its ears are lying flat back against its head. It was caught in December together with the mother and apparently still an exclusive suckling. There is no accurate way yet to determine the age of specimens like this juvenile. There are strong indications that fruit bats of various species, among which *Rousettus aegyptiacus* (Geoffroy Saint-Hilaire, 1810), are weaned at an age of at least four months (see Bergmans, 1979), but our paratype is most certainly younger than that. Data on *Lissonycteris angolensis* (Bocage, 1898), a fruit bat of nearly the same size as *Rousettus spinalatus,* suggest that while at birth young ones have forearm lengths of about 40% of that of the mother, they may still be exclusive sucklings when this has increased to about 75% (Bergmans, 1979, and unpublished notes). If, with a forearm of about 67·5% the length of its mother's forearm, the paratype may be assumed to have been in its second or third month, birth will have occurred in September or October.

ECOLOGY. The specimen of *Rousettus spinalatus* from Niah Great Cave, Sarawak, Borneo, was caught in the cave mouth. Like other *Rousettus* species, *spinalatus* may be expected to roost in caves.

PARASITES. A spinturnicid *Meristaspis lateralis* (Kolenati, 1856) (Acari) was collected from one of the axillar endopatagium pockets of the paratype. This mite is known from several other species of *Rousettus* and also from a number of the other genera of the Pteropodidae.

Discussion

Type locality. The holotype and its young were collected by natives working for a German dealer residing in Medan. Most of their specimens are from in or around this city, but some of their material was reported to originate from Prapat (or Prabat) at Lake Toba, at an altitude of about 2000 m. As none of their specimens bears a field label, all are from 'Medan or Prapat' (Dr K. Bauer, *in lit.,* 28 July, 1978). Most mammal collecting on Sumatra has been done in lowland areas, which until now have yielded few specimens of *Rousettus.* One might therefore seriously consider Prapat as potential type locality, and subsequently the species as possibly montane. However, this would be contradicted by the sparse fur of the two Sumatran specimens, and by the collection of the specimen from Niah Great Cave, a lowland site near the coast of Sarawak, Borneo. Incidentally, lowland fruit bat species do penetrate mountain forests, and the matter of the type locality cannot yet be decisively settled. (Our reason for not using the Sarawak specimen as type is that this is only subadult).

Relationships. Of all the known recent species of *Rousettus* only *R. amplexicaudatus* sensu lato shows a degree of morphological and dimensional similarity to *R. spinalatus,* and may well be regarded as its closest living relative in a phylogenetic sense. At the same time, the differences between the two species are distinct and constant, and independent evolution over a considerable stretch of geological time may be assumed. The holotype specimen of *spinalatus* has been compared directly with specimens of *amplexicaudatus* from Timor (its type locality; efforts to trace the actual type specimen in the Muséum National d'Histoire Naturelle in Paris, late in 1978, have failed), Sumatra, Enggano, Lang Island, Java, Nusa Penida, Pulau Peleng, Talisai (or Talise), New Guinea and the Philippines, all from the collections of the Museum Zoologicum Bogoriense at Bogor, the Rijksmuseum van

Natuurlijke Historie at Leiden, and Zoölogisch Museum in Amsterdam. Moreover, some alcoholic specimens from Cambodja in the Muséum National d'Histoire Naturelle in Paris and some dry specimens from Bangkok, Java, Bali, Nusa Penida and Timor in the Zoologisches Museum in Berlin have been studied. Additional specimens from Alor and Savu Islands, Sumatra, Enggano, Borneo, the Philippines and from Thailand in the collections of the British Museum (Natural History) have also been examined and measured.

The most useful distinguishing characters of *spinalatus* are the high wing insertion, the backward position of M^2 (possibly related to an average greater relative length of the upper tooth row), and the morphology of a number of teeth. All specimens of *amplexicaudatus* have a distinct band of dorsal fur in between both endopatagial insertions, varying in width from 15 to 35·5 in the dry skins of the specimens examined (Table 1), whereas in *spinalatus* there is no such band (Fig. 1). The shortest distance between M^2 and the margin of the palate where it passes into the rear of the zygomatic arch insertion (Figs 5a, b) is 0·7 in the holotype of *spinalatus,* and varies from 1·3 to 2·5 in *amplexicaudatus* (Table 1). The dentition of *spinalatus* shows the following differences (Figs 2–5): its upper incisors are more delicate; C^1 is distinctly shorter, not as laterally compressed, with an egg-shaped instead of subelliptical outline, and has much more of a lingual shelf; P^3 is slightly shorter, anteriorly not as laterally compressed, with its greatest width in the middle instead of in the anterior part, not as strongly tapering toward its posterior end, and without an inward curve in the back half of its outer ridge profile; the antero-internal corner of P^4 scarcely protrudes forward, its postero-internal corner not reaching as far back as its postero-external corner, and its outer ridge is lower, with a more simple profile; M^1 is slightly narrower, with a somewhat more salient antero-internal corner and also a lower and simpler outer ridge; M^2 is somewhat longer and wider, with a lower and simpler outer ridge; its lower incisors are smaller; C_1 is also less bulky, and lacks a vertical anterior keel; P_1 is shorter and narrower; P_3 is shorter and has a less sharp, more vertical anterior keel; P_4 is shorter, without a distinct anterior vertical keel, and with the postero-external corner extending further backward than the postero-internal corner; M_1 is somewhat shorter; M_2 is either slightly shorter, equal in length, or somewhat longer; M_3 is longer and wider.

Larger series of *spinalatus* may reveal other distinctive features. For instance, its mandibular height, measured as indicated in Fig. 3, may average higher than in most *amplexicaudatus* populations (see Table 1).

Sympatric *Rousettus* species. Hitherto, few Sumatran representatives of the genus *Rousettus* have been recorded. Temminck (1825) recorded *Pteropus amplexicaudatus* Geoffroy Saint-Hilaire (= *Rousettus*) from 'Sumatra', but does not specify the material on which this was based. From his text it may be inferred that this must have been either the adult female or the young specimen which he stated to be in the collection of the Rijksmuseum van Natuurlijke Histoire at Leiden. Jentink (1887) listed, as specimen d, an adult skeleton as the sole Sumatran representative of *Rousettus amplexicaudatus* in this collection, which may have belonged to Temminck's specimen. Another reference to Sumatran *R. amplexicaudatus* appeared in Dobson (1878) under *Cynonycteris amplexicaudata.* This was based on a specimen from 'Sumatra' in the British Museum (Natural History) (38.3.13.36), which Andersen later (1912 : 43 and 812) referred to the nominate subspecies. (As is obvious from his hand-writing on the label of the Leiden specimen mentioned above, Andersen had also seen this example, and identified it likewise.) In the course of the present study, both specimens have been re-examined, and both were found to represent *amplexicaudatus.* We are not aware of any published record of Sumatran *Rousettus* other than the ones mentioned, and it seems useful to mention here other species and specimens which have recently come to our knowledge.

Rousettus leschenaulti (Desmarest, 1820)

Kalianda, South Sumatra: 1 ♂, skin and skull, 2 August 1934, leg. J. J. Menden (Zoologisches Museum Berlin 39608); forearm length 90·9, greatest skull length 42·1, condylobasal length 40·9. Its teeth are too worn to allow measuring.

Table 1 Comparative measurement ranges (in millimetres) of the holotype of *Rousettus spinalatus* n.sp. and of *Rousettus amplexicaudatus* (Geoffroy Saint-Hilaire, 1810).

	Width of dorsal fur band at level of elbows when pressed against body				Shortest distance of M² to margin of lateral palate/zygomatic arch				C¹–M² length as percentage of condylobasal length				Height of mandibulum as percentage of its length			
	♂♂		♀♀		♂♂		♀♀		♂♂		♀♀		♂♂		♀♀	
	n	min.–max.	n	min.–max.	n	min.–max.	n	min.–max.	n	min.–max.	n	min.–max.	n	min.–max.	n	min.–max.
R.spinalatus																
holotype			1	0			1	0·7			1	38·6			1	43·4
subadult from Sarawak			1	0			1	0·6			1	40·0				
R. amplexicaudatus																
Sumatra			1	31			2	1·3–1·3			1	±35·3			2	37·1–38·6
Thailand	1	20			1	1·3	1	1·3					1	43·0		
Cambodja	1	19·5	1	21												
Enggano	1	30	1	22·5	1	2·1	2	1·7–1·8			1	36·1	1	40·5	2	39·9–40·9
			1*	20												
Lang Island	2	19–23	2	18–19	2	1·6–1·6	2	1·6–1·9	1	37·2	2	36·5–38·5	2	39·0–41·6	2	41·7–43·0
Java	6	17–35·5	14	12·5–33·5	6	1·4–1·9	9	1·4–2·0	5	35·1–38·3	8	35·3–37·7			6	38·5–41·3
Bali			1	18												
Nusa Penida	2	26–29·5	1	28	1	2·4	1	1·6	1	36·9	1	35·0				
Alor Island	1	15·5	1	21	1	1·8	1	1·3	1	35·9	1	35·3	1	39·4	1	42·0
Savu Island			1*	18			1	1·5			1	36·7			1	39·4
Timor	8	20·5–29·5	9	21–27·5	2	2·0–2·4	5	1·6–2·0	2	35·9–36·2	5	34·7–38·1	1	40·2	4	37·9–40·4
Borneo	3	27·5–30			1	2·0			1	34·8			1	44·1		
	1*	23			1	1·4			1	36·5			1	42·2		
Talisai	1	20·5			1	2·5										
Pulau Peleng	1	15			1	1·6							1	42·8		
New Guinea			1*	20·5							1	35·9				
Philippines	3	15–23·5	3	16–19	3	1·6–2·3	4	1·6–1·9	2	34·0–35·6	3	35·2–37·8	2	43·3–43·9	3	39·7–41·6
			1*	17												

*Specimens in alcohol (all others: dry skins)

From its measurements, this specimen, which is the first of this species recorded for Sumatra, seems to link the western nominate race with the larger, eastern subspecies *shortridgei* Thomas & Wroughton, 1909, from Java.

Rousettus species
According to Boeadi (*in lit.*, 22 March, 1979) there are in the Museum Zoologicum Bogoriense at Bogor about 27 Sumatran *Rousettus* specimens from Lampong, South Sumatra, and upper Siak-Kampar rivers, Central Sumatra, of which the specific identity has not yet been determined.

Of course, actual sympatry of *spinalatus* with either *amplexicaudatus* or *leschenaulti* on Sumatra has yet to be proven.

The specimen of *Rousettus spinalatus* from Sarawak, Borneo was first recorded as *R. amplexicaudatus* by Harrisson (1967: 229). This specimen, taken 'low off floor' in the West Mouth of Niah Great Cave, is now BM(NH) 75.589. The other specimen that he records, a male, taken about six weeks previously on the same spot and now BM(NH) 69.221, actually represents *R. amplexicaudatus.* Thus, at Niah at least both species occur sympatrically. *R. amplexicaudatus* has also been recorded from Sabah and West Kalimantan (Medway, 1977 : 39).

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Relationships between hummingbirds and flowers in the Andes of Colombia

David W. Snow & Barbara K. Snow

Zoology series Vol 38 No 2 27 March 1980

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Relationships between hummingbirds and flowers in the Andes of Colombia

David W. Snow and Barbara K. Snow
Department of Zoology, British Museum (Natural History), Cromwell Road, London
SW7 5BD

Synopsis

An account is given of the feeding ecology of hummingbirds in the Eastern Andes of Colombia, based on nine weeks of field work in 1978. Three hummingbird communities were studied, two in the temperate and one in the subtropical zone. The 25 species of hummingbirds observed showed very different degrees of specialization for exploiting the nectar of particular kinds of flowers, from an extreme in *Ensifera,* which appears to have coevolved with and to be dependent on species of *Passiflora,* to generalists which share their nectar sources with other hummingbirds and insects. In the light of these observations we discuss the 'syndrome of ornithophily', the alternative foraging strategies of trap-lining and territoriality, nectar characteristics, and the evolution of ornithophily in the Andean flora.

Introduction

The ecology of hummingbirds has been the subject of much research in the last ten years, with the emphasis on three related aspects: energetics, the structure of local hummingbird guilds (with which may be included flower-piercers and other nectarivores), and coevolutionary relationships between hummingbirds and their food plants. Undoubtedly a prime reason for the popularity of hummingbirds for this kind of research is the fact that under favourable conditions, in the field, quantitative assessments can be made both of their expenditure of energy, of the availability of nectar from different plants, and of the birds' efficiency in obtaining nectar. As a result, tremendous advances have been made in our understanding of the biology of hummingbirds. Stiles (1980) gives a review, with key references.

In comparison with the energetic aspects of hummingbird ecology and with studies of interactions between guild members, coevolutionary relationships have tended to take a subordinate place, a notable exception being the analysis by Stiles (1975) of the relationship between hermit hummingbirds and *Heliconia* species in a lowland forest in Costa Rica. Most field studies have been carried out at high altitudes in Central America, where a relatively small number of hummingbird species coexist. Nothing has been published so far on relationships between hummingbirds and their food plants in what may be called the core area of hummingbird evolution, the subtropical and temperate forests of the Andes from Colombia to Peru, where the greatest number and variety of hummingbird genera and species coexist. It was for this reason that we attempted a survey of the feeding ecology of hummingbirds in the Eastern Andes of Colombia in July and August 1978, the results of which are presented in this paper.

It must be stressed at the outset that our findings represent the merest scratching at the surface of a subject of great complexity. Our observations extended over only two months, with a span of only three weeks in each of the three areas (two forest, one farmland) in which we worked; but even in that time in all three areas there were significant changes in the availability of nectar, as some plants finished and new ones came into flower. In any area, field work must obviously be continued over at least a complete year in order to get an adequate idea of the food resources available to hummingbirds. In addition, the vegetation was almost entirely different in the two forest areas, about 150 km apart, and the hummingbird species were largely different. Many areas would have to be sampled in order to get an adequate idea

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of the overall distributional pattern of vegetational communities and their associated hummingbirds, even in a small section of the Andes.

Recent research on hummingbird ecology has revealed an important distinction between two fundamentally different feeding strategies. A hummingbird may defend a feeding territory, usually a concentrated source of nectar of small extent such as a single profusely flowering tree, or it may make the rounds of many scattered sources of nectar which it does not attempt to defend, a strategy generally known as 'trap-lining'. Territorial hummingbirds are usually unspecialized feeders, not closely adapted to feeding at particular kinds of flower; trap-lining hummingbirds are typically specialists, adapted to visiting a few kinds of flowers. This division of feeding strategies will be discussed later with reference to our observations in the Andes; we mention it here as we refer to trap-lining and territorial feeding in the species accounts that precede the discussion.

Study areas

Our original intention was to spend the whole of our time in one area, on the eastern slopes of the Eastern Andes, quite close to Bogotá. Owing to unforeseen circumstances we were forced to leave this area half way through the period, and moved to another locality about 150 km to the NNE, on the western slopes of the Eastern Andes, where observations were made in two areas several kilometres apart. The three study areas (referred to in what follows as Fonté, Carare and Togui) are briefly described below. The first two are in the lower part of the Temperate Zone, as defined by Meyer de Schauensee (1964), and the third is near the lower limit of the Subtropical Zone.

> Slopes of Cerro Fonté, Vereda de Ferralarada, Municipio de Choachí, Cundinamarca (4° 32′ N, 73° 51′ W), 2400–2550 m; 3–25 July. Gently sloping, western-facing mountainsides, partly wooded, partly cleared for primitive agriculture (pasture, small fields of potatoes and maize), cleared areas in places reverting to bushy secondary growth. Woods mostly with trees not over 15 m in height (perhaps secondary, resulting from earlier clearances).
>
> Slopes of Cerro Carare, 9 km ESE of Togui, Mun. Togui, Boyacá (5° 54′ N, 73° 25′ W), 2300–2500 m; 29 July–3 August, 14–22 August. Natural forest on gentle or moderate slopes, thinned in places by extraction of larger trees, with open areas (some cleared for farming, some probably naturally unforested, due to poor drainage).
>
> Hacienda Versalles, near Togui, Boyacá (5° 55′ N, 73° 32′ W), 1700 m; 27–30 July, 4–14 and 23–24 August. Cattle farm with sugar cane, maize and 3 small patches of coffee, natural vegetation almost entirely gone; trees confined to strips along river banks and between fields; *Eugenia jambos* (introduced) more abundant than any other tree.

Methods

A special effort was made to find all the flowers that were being fed at by hummingbirds in each area at the time of our visits. Flowers were measured (internal length of tubular part of corolla, from opening to base), and measurements were made of nectar concentrations and rates of nectar production. Nectar was extracted with disposable micropipettes (manufactured by Camlab, Cambridge, England) of various capacities (5 to 100 µl), and sugar concentrations were measured with a Bellingham & Stanley pocket refractometer calibrated from 0 to 50%. Percentage concentrations were not compensated for temperature, but at the temperatures and concentrations recorded compensations are all below 0·4% and thus negligible. To measure nectar production rates, flowers were drained of nectar and then bagged, so as to be inaccessible to birds over the period of the measurement.

Observations of the feeding behaviour of hummingbirds were made with 8× and 10× binoculars, usually at fairly close quarters. Some observations were 'casual', i.e. made during random walks in the area, during which all observed feeding was recorded; but most were made during timed watches at nectar sources which we had found to be, or suspected to be, important. Each visit by an individual hummingbird to one plant or (in the case of some herbaceous plants, small bushes and clumped trees) group of plants was counted as a unit for purposes of tabulation. When practicable, stop-watch timings were made of the rate at which flowers were visited, and the number and duration of probes into individual flowers.

A limited number of hummingbirds were caught in mist-nets, weighed, measured, and marked with quick-drying paint (dope), mainly on the central tail-feathers, or with coloured inks on white or pale parts of the plumage, for future identification in the field.

Specimens of food plants were collected, and have been deposited in the Herbarium of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia.

The hummingbirds

On the basis of Meyer de Schauensee's (1964) statements of ranges and altitudinal zones of hummingbirds in Colombia, a potential total of 21 species might occur in the Temperate Zone in the vicinity of Carare and Fonté. Five of these were not to be expected in our study areas, as they are birds of open country or of the upper part of the Temperate Zone, above the level where we worked. Of the remaining 16 species, we recorded 14 in one or both of our study areas. The two species not recorded were *Coeligena bonapartei,* which might have occurred at Carare, and *Ramphomicron microrhynchum,* which might have occurred in both areas.

Again on the basis of Meyer de Schauensee's statements, there are 18 species that reach their upper limits in the Subtropical Zone and, from their geographical ranges, might have been expected in at least one of our study areas. Of these, five were recorded in the Carare and/or Fonté study areas, and four more at Togui. Hence our sampling of the more strictly subtropical hummingbirds was much less complete than our sampling of the temperate species, as would be expected from the fact that our two main study areas were at lower temperate levels and the subtropical Togui study area had very little natural vegetation.

All the species recorded are listed, together with weights and measurements, in Table 1.

Observations at Fonté

Vegetation, and available nectar sources

As already mentioned, the woods in the Fonté study area consisted mainly of rather small trees, not over 15 m in height, and may mostly have been secondary, resulting from earlier clearances. Some tracts, consisting almost entirely of one species of Melastomataceae, were certainly secondary. In some places the undergrowth of unfenced woods had been badly damaged by cattle infiltrating from adjacent pastures. In some rocky and steep places the trees were higher and more massive, and the vegetation probably approximated to the natural condition.

Very few of the canopy trees had flowers attractive to hummingbirds at the time of our visit; the only two that were found, *Symplocos mucronata* and an unidentified species, were both uncommon. Epiphytic bromeliads of several species were numerous on the larger trees, but were not in flower at the time of our visit.

The under-storey of the woods in the lower part of the study area consisted largely of slender, straggling trees of a single species, *Palicourea angustifolia,* which were in flower at the time of our visit and were the most important nectar source for the unspecialized hummingbirds. This tree was much less abundant in the upper part of the area, where another, larger species of *Palicourea* was fairly common. This latter species, *P.* cf. *anacardifolia,* had just finished flowering at the time of our visit and most trees had unripe fruit; almost certainly it had been an important nectar source in the period immediately before our arrival. The only other under-storey trees and shrubs seen to be fed at by hummingbirds were: *Symbolanthus tricolor,* a sparsely distributed straggling shrub; *Psychotria* cf. *aschersonianoides,* a small locally common shrub; and *Cinchona* cf.

Table 1 Wing-lengths, bill-lengths and weights of hummingbirds recorded at Fonté (F), Carare (C) and Togui (T)

	Area	Wing mm	Bill (exposed culmen) mm	Bill as % of wing	Weight g
Doryfera ludoviciae	C	60·0	32·9	54·8	5·7
Phaethornis guy	T	61·3	44·3	72·3	5·2
Colibri thalassinus	C	65·6	20·8	31·3	5·3
Colibri coruscans	FC	77·2	24·2	31·3	7·8
Anthracothorax nigricollis	T	65·7	24·8	37·7	7·0
Chlorostilbon gibsoni	T	46·1	16·2	35·1	3·1
Chlorostilbon poortmani	FC	42·5	16·5	38·8	—
Amazilia franciae	T	53·6	24·3	45·2	5·0
Amazilia cyanifrons	T	54·5	17·8	32·6	5·0
Amazilia tzacatl	T	55·0	20·4	37·1	4·8
Adelomyia melanogenys	CT	52·8	15·2	28·8	4·2
Lafresnaya lafresnayi	F	61·7	25·2	40·8	5·9
Coeligena prunellei	C	77·8	29·8	38·3	7·4
Coeligena helianthea	F	71·6	29·9	41·8	—
Coeligena torquata	C	75·5	33·0	43·7	7·0
Ensifera ensifera	F	76·5	83·1[1]	108·6	12·5
Boissoneaua flavescens	C	76·7	17·9	23·3	8·6
Heliangelus amethysticollis	FC	64·3	18·0	28·0	5·9
Eriocnemis vestitus	F	59·3	18·3	30·9	4·9
Eriocnemis cupreoventris	F	61·6	18·6	30·2	5·6
Ocreatus underwoodi	C	43·1	14·0	32·5	3·1
Lesbia nuna	F	50·7	10·0	19·7	—
Metallura tyrianthina	F	53·8	11·0	20·4	3·4
Aglaiocercus kingi	C	53·5	15·2	28·4	4·4
Acestrura mulsant	FCT	40·4	16·7	41·3	3·2

Note: All figures are means. Sexes are combined. Measurements are from museum specimens from the Eastern Andes of Colombia, supplemented by data from this study. Weights are from this study, supplemented by data from Greenewalt (1962), Miller (1963), Carpenter (1976) and Feinsinger *et al.* (1979).

[1] Bill-length very variable, up to c. 105 mm. Effective length for probing tubular flowers is about 10 mm greater than bill-length, owing to marked narrowing of the skull towards the base of the bill.

pitoyensis, a rather uncommon tree in the upper part of the study area. Among the vines, *Pentadenia strigosa* was common in all the woods with undisturbed undergrowth. Its large orange flowers, borne almost from ground level up to about 5 m, were conspicuous in the woody and mossy undergrowth.

Along wood-edges and in more open, rocky areas an ericaceous shrub, *Cavendishia cordifolia,* was locally abundant and in flower. As a nectar source for several hummingbird species it was second only to *Palicourea angustifolia.* Only two other ericaceous plants were found in flower, *Disterigma alaternoides,* which was rare, and a single example of an unidentified species. The poverty of the Ericaceae was in marked contrast to their richness and abundance at Carare (p. 117).

In bushy second growth, especially along edges, several hummingbird flowers were fairly abundant. *Castilleja fissifolia,* a scrambling shrub, was common in such places. *Passiflora mixta,* a vine with very long tubular flowers, was more local but conspicuous where present. An abundant low scrambling shrub, *Siphocampylus bogotensis,* began to come into flower about half way through our visit. *Manettia coccocypseloides,* a climber with small white flowers, was more local. Blackberries, *Rubus* spp., were abundant and in all stages of flower and fruit. *Cuphea dipetala,* a slender shrub, was generally distributed in bushy areas but sparse. *Rubus* and *Cuphea* also grew as low plants out in the open in neglected fields.

Table 2 Characteristics of hummingbird flowers, Fonté

			Corolla		Nectar		
		length of tube (mm)	colour	orientation[1]	concentration[2] %	production (µl) per hour[3]	per 24 hrs[4]
Theaceae	*Symplocos mucronata*	10	pink	H	—	—	—
Passifloraceae	*Passiflora mixta*	114	pink	H	22–30, 25·5	12·0 (max 32·2)	506
Ericaceae	*Cavendishia cordifolia*	15	pink & white	H–P	9–22, 14·9	1·2 (max 4·0)	22·3
	Disterigma alaternoides	7	white	H	—	—	—
Rosaceae	*Rubus* sp.	nil	pink & white	H–U	—	—	—
Lythraceae	*Cuphea dipetala*	18	mauve	H	33	—	—
Tropaeolaceae	*Tropaeolum tuberosum*	24	orange	H	—	—	—
Gentianaceae	*Symbolanthus tricolor*	36	pink	H	19	1·5	—
Scrophulariaceae	*Castilleja fissifolia*	19[5]	green (calyx red)	H	16–23, 18·7	—	11·0
Gesneriaceae	*Pentadenia strigosa*	28	orange	H	24–31, 27·0	—	33·5
Campanulaceae	*Siphocampylus bogotensis*	55	red	H	21	1·0	32·5
Rubiaceae	*Manettia coccocypseloides*	12	white	H	—	—	—
	Palicourea cf. *anacardifolia*	20	yellow	H	—	—	—
	Palicourea angustifolia	13	mauve	H	10–18, 13·8	1·0 (max 3·9)	29·5
	Psychotria aschersonianoides	6	white	H	—	—	—

Notes: [1] H = horizontal; P = pendent; U = upright.
[2] range and mean. Single figures indicate single measurements.
[3] mean (and maximum recorded)
[4] maximum recorded; for further details, see text.
[5] length of closed tube; see text.

No other plants were important nectar sources at the time of our visit. Over 99% of all hummingbird feeding records were from the plants mentioned above. Flower and nectar characteristics of the majority of them are given in Table 2, and further details of the most important of them are given in the following section.

The most important nectar sources

Palicourea angustifolia

The tubular mauve flowers are borne in racemes. Most racemes did not hold more than 6 open, nectar-producing flowers at a time. Individual flowers lasted 2–3 days. The figures for nectar concentration given in Table 2 are based on 46 out of 50 readings, four very low readings being omitted (5–9%). Concentrations tended to be higher in the early morning (14–18%) than at midday or in the afternoon (10–16%). There was also some decrease in concentration with the age of the flower: the last readings for 6 flowers, immediately before the end of their nectar production, averaged 11% (range 6–13%). Nectar production rates also were highest in the morning, the average for 12 morning rates being 1·23 μl/hr, while rates for the whole day averaged 0·97 μl/hr. Hourly rates for the night (which included the early evening and very early morning) averaged 0·41 μl/hr. The maximum figure for nectar production over 24 hours given in Table 2 (29·5 μl) was approached by two others (28·5, 27·9), while three others were considerably lower (21·5, 13·8, 9·1). Age of the flowers might largely have accounted for these differences.

Because of its abundance, the considerable number of flowering racemes on even quite small plants, and its short corolla tube, *Palicourea angustifolia* offered an abundant nectar supply to the shortest-billed of the hummingbirds, as well as to those with longer bills. Several timings of *Eriocnemis vestitus* showed that it visited *Palicourea* flowers at a rate of one flower every 1·3 s (combined figures, 141 flowers in 178 s), and this rate seemed typical of the smaller hummingbird species. As mentioned later, four species of hummingbirds maintained feeding territories at *Palicourea* clumps.

Cavendishia cordifolia

The tubular, pale pink and white flowers of this heath are borne in terminal clusters, protected by scaly sheaths of pink bracts. Individual flowers last 2–3 days. The figures for nectar concentration given in Table 2 are based on 32 of 36 readings, the four omitted being abnormally low (2–6%). The nectar concentration of individual flowers was rather consistent over 2 or more days (i.e. some had consistently high, and some low concentrations), with a tendency for concentrations to decrease very slightly in the course of a day (by 0·6%, average of 10), and from one day to the next (by 1·5%, average of 6).

As already mentioned, *Cavendishia* was second in importance only to *Palicourea* as a nectar source for several hummingbird species. The richest feeding areas for these birds were along wood-edges, where both *Palicourea* and *Cavendishia* frequently grew side by side.

Castilleja fissifolia

The flowers are borne in terminal spikes, the pale green corolla being ensheathed along most of its length by the calyx whose distal half is red. The corolla is slightly curved along its whole length; it is tubular basally (for the proximal 20 mm), but distally is split along the under-side (for the distal 25 mm). In spite of many attempts, we never found it easy to extract much nectar from *Castilleja* flowers. Recorded nectar concentrations were 23, 17 and 16%. The maximum figure for nectar production over 24 hours was 11 μl; other figures were 8, 6 and 1 μl.

Castilleja was one of the preferred flowers of *Lafresnaya lafresnayi,* whose curved bill fits the corolla exactly. Almost certainly *Lafresnaya* is the plant's chief pollinator, as was indicated by the pale pollen that conspicuously coated their foreheads when they were feeding on it. The only other hummingbird seen to visit *Castilleja* flowers, *Lesbia nuna,* has a much shorter, straight bill. It either probed the flowers at the base of the split in the corolla, about 19 mm from the nectary, or pierced the base of the calyx, on the upper side. Neither method would bring it into contact with the anthers or stigma.

Passiflora mixta

The long tubular flowers, with a ring of pink petals round the entrance to the tube, arise singly from leaf axils near the growing tip of the long climbing and sprawling stems. Along each stem only one or two flowers are open and producing nectar at any time, those that are distal being in bud and those that are proximal in fruit. Each flower usually lasts 4–5 days (extremes of 3 and 6 recorded). The figures for nectar concentration in Table 2 are based on 19 out of 22 readings, the three omitted being very low (17–18%). Two of the very low readings, and perhaps the third, were from flowers that were nearly over. (A reading of 12% from a flower that was already withered is also omitted). Nectar concentrations remained rather steady throughout the day; but measurements of individual flowers on successive days indicated that concentration rises and then falls during the life of the flower. Nectar production is copious, but also very variable, the maximum amount produced in 24 hours shown in Table 2 (506 μl) being a good deal more than the next highest (397 μl). A younger flower on the same plant as the latter produced only 81 μl on the same day in the same 24-hour period. Another flower produced 98 μl in one 24-hour period, and 150 μl in the next.

Ensifera ensifera is the only hummingbird that we saw taking nectar 'legitimately' from *Passiflora mixta,* i.e. by entering through the opening of the corolla tube, and in fact is the only one that could possibly do so, its effective bill length (Table 1) being almost the same as the *Passiflora* corolla tube. Practically all the *Passiflora* flowers in the study area were, however, pierced at the base by the flower-piercer *Diglossa albilatera,* and hummingbirds of several species extracted nectar from the holes made by *Diglossa.* Consequently, unprotected *Passiflora* flowers usually contained very little nectar. The effect of this nectar 'thieving' on *Ensifera* is discussed later (p. 115).

Pentadenia strigosa

This climbing plant was abundant in shady places, especially among rocky outcrops. It flowered as low as a few cm from the ground in dense second growth and up to 5 m where it had clambered up trees in older woodland. The flowers grow in pairs along the stem, both members of a pair opening at about the same time; they last 7–8 days and are protandrous. The hairy orange corolla is in the form of a wide tube (28 mm long, 18 mm deep), decurved distally and opening downwards, and is borne horizontally, suspended at the end of the long, vertically hanging pedicel.

Only *Lafresnaya* females were seen feeding at *Pentadenia* flowers; no flower-piercers were seen to visit them and no pierce holes were found on the flowers examined. Several features of the flower suggest adaptations protecting the nectar against flower-piercers: the delicate suspension of the flower at the end of the long pedicel, which would make it difficult to perch on and inaccessible from other perches, and the wide, rounded corolla tube, which would be difficult for a flower-piercer to grasp and pierce.

Symbolanthus tricolor

The pink flowers, with darker pink streaks, are borne very sparsely, only 1–4 being open at a time on the few plants that were seen. The nectaries are protected by the tough thick calyx base. Only a single reading of nectar concentration was made, and one measurement of rate of nectar production (Table 2). Two hummingbird species, *Coeligena helianthea* and *Lafresnaya,* were seen visiting these flowers.

Siphocampylus bogotensis

Little information was obtained on this plant, as its flowering season was only just beginning when we left the area. The nectar concentration and production rates given in Table 2 are based on single measurements. It seemed very likely that *Siphocampylus* was going to be an important nectar source for *Lafresnaya,* the only hummingbird species seen to visit it. The corolla length and curvature fit *Lafresnaya*'s bill closely. The flowers are soft, with no protection of the nectaries, and preliminary observations indicated that *Diglossa albilatera* regularly pierced them at the base.

Feeding ecology of the hummingbirds

Of the 11 species of hummingbirds recorded on Fonté, all but two were regularly present and seen whenever watches were kept at appropriate flowers. The two exceptions were *Acestrura mulsant,* which was seen only once, and *Colibri coruscans,* which was abundant at lower levels (below c.2200 m) but only once seen at the lower edge of our study area. The nine resident species can be divided into three groups: four medium-sized to small woodland species with short, straight bills, which held territories centred on food plants with short corolla tubes *(Heliangelus amethysticollis, Eriocnemis cupreoventris, E. vestitus, Metallura tyrianthina);* three larger, long-billed species of woodland or woodland edge, feeding mainly or entirely on specialized hummingbird flowers and non-territorial *(Lafresnaya lafresnayi, Coeligena helianthea, Ensifera ensifera);* and two small open-country species *(Lesbia nuna, Chlorostilbon poortmani).* The feeding records for these hummingbirds are summarized in Table 3.

Three species of flower-piercers (*Diglossa* spp.) occurred in the study area, two of which exploited hummingbird flowers. One of them, *D. albilatera,* was abundant and had a significant effect on the feeding ecology of the hummingbirds with which it competed for nectar.

Table 3 Hummingbird feeding records, Fonté

	C.p.	*L.l.*♂	*L.l.*♀	*C.h.*	*E.e.*	*H.a.*	*E.v.*	*E.c.*	*L.n.*	*M.t.*
Shrubs and scramblers										
Cavendishia cordifolia	1	1		16		5	11	13	4	3
Rubus sp.				3					6	16
Cuphaea dipetala	1		1					1	7	1
Symbolanthus tricolor			5	6						1[1]
Castilleja fissifolia		1	17						35[1]	
Siphocampylus bogotensis		1	6							1[1]
Psychotria aschersonianoides										6
Vines/climbers										
Passiflora mixta				29[1]	10		1[1]	3[1]		29[1]
Pentadenia strigosa			8							
Manettia coccocypseloides										7
Trees										
Cinchona cf. *pitoyensis*										1
Palicourea cf. *anacardifolia*				1						1
Palicourea angustifolia	1	23	4	5		21	6	12	3	69
Other plants	2	3	1	1						7
Insect-hawking		2	2				1	7	16	5
Totals (453)	5	31	44	61	10	26	19	36	74	147

Hummingbirds abbreviated as follows: *C.h., Coeligena helianthea; C.p., Chlorostilbon poortmani; E.c., Eriocnemis cupreoventris; E.e., Ensifera ensifera; E.v., Eriocnemis vestitus; H.a., Heliangelus amethysticollis; L.l., Lafresnaya lafresnayi; L.n., Lesbia nuna; M.t., Metallura tyrianthina.*

Note: [1] nectar taken 'illegitimately', through hole in corolla base.

Heliangelus amethysticollis
Eriocnemis cupreoventris
Eriocnemis vestitus
Metallura tyrianthina

These four straight-billed, medium-sized to small hummingbirds are treated together, as all fed largely on *Palicourea angustifolia* and (especially *Eriocnemis* spp.) on *Cavendishia cordifolia,* and individuals of all four held feeding territories centred on these plants. They frequently came into conflict with one another, dominance relations being in accordance with their size, i.e. in the order in which they are listed above.

A small wood, measuring about 100 by 30 m (0·3 ha), surrounded on three sides by pasture and on the fourth by scrub, with an under-storey consisting largely of *Palicourea* while *Cavendishia* grew abundantly along the edges, contained an extraordinary number of hummingbirds of these four species for the first two weeks of our visit. Towards the end, the flowering season of *Palicourea* appeared to be coming to an end and the number of hummingbirds decreased. Accurate censusing was not possible in the dense growth within the wood, but probably at least 25 birds were present around the middle of July. Trapping also gave some idea of the numbers. Nine different individuals were caught in two 13-m mist-nets set within the wood on 10–11 July (2 *Heliangelus,* 4 *E. cupreoventris,* 1 *E. vestitus,* 2 *Metallura*), and on 18 July nets set in the same positions caught six different birds (1 *Heliangelus,* 3 *E. cupreoventris,* 2 *Metallura*), all except one *Metallura* different from the individuals caught a week earlier. Several hours were spent in looking for marked birds 2–4 days after the netting operations, but only three marked individuals were seen among the many that were examined. It seemed that individuals were holding very small feeding territories, many of them perhaps rather briefly. There was much trespassing and chases were very frequent, especially early in the period, but were almost always impossible to follow for more than a second or two. Two *Heliangelus* territories (one in an adjacent wood with similar vegetation) consisted of (1) several *Palicourea* bushes spread over a space of 10 by 9 m, and (2) two *Cavendishia* bushes about 10 m apart.

In an even smaller copse, roughly circular and about 25 m in diameter, with sparse *Palicourea* in the under-storey and a few *Cavendishia* bushes round the edge, a single male *E. vestitus* held a territory from 7 to 21 July, effectively excluding other hummingbirds from the area. It also chased intruding White-sided Flower-piercers *Diglossa albilatera,* which were present in all the larger woods, so persistently that it effectively excluded them, thus maintaining its nectar resources intact. On 22 July, when the number of *Palicourea* flowers had declined somewhat, it disappeared and its place was taken almost immediately by a *Metallura,* which occupied the area and patrolled it much as *E. vestitus* had done, but was unable to prevent occasional visits by *Lafresnaya* and *Lesbia nuna.* It seemed that the nectar supply had become insufficient to maintain *E. vestitus* but could still maintain the smaller *Metallura.*

There were some differences in habitat preference between these four hummingbirds. We did not record *Heliangelus* outside more or less closed woodland, whereas *E. cupreoventris* and *Metallura* showed some preference for woodland edges, at times coming well into the open. Rather few observations were made of *E. vestitus,* the least common of the four species (as the trapping figures indicate), but from the records it appeared to favour more open habitats than the others. This is consistent with its general distribution: according to Meyer de Schauensee (1964) it is a bird of the temperate and lower páramo (i.e. more open) zones, whereas *E. cupreoventris* is a bird of the subtropical (more densely wooded) and temperate zones. Among the species that we observed, they were the only examples of overlap between two closely related species with different altitudinal preferences.

Some of the differences between the feeding records for the four species probably resulted from these differences in habitat preference; for instance the marked preponderance of feeding at *Palicourea* by *Heliangelus,* which fed within the woods, compared with the slight preponderance of feeding at *Cavendishia* by the two *Eriocnemis* species, which fed more in the open. The lack of records of *Heliangelus* feeding at *Passiflora* may have the same explanation. The very few records of feeding at *Cavendishia* by *Metallura,* however, indicate active avoidance of *Cavendishia* flowers, whose 15 mm corolla tubes may be too long for efficient probing by *Metallura*'s 11 mm bill. *Metallura* showed much the greatest variety in its nectar feeding of all the species in the area (Table 3), especially in visiting small flowers not seen to be visited by other species *(Psychotria, Manettia, Symplocos).*

Lafresnaya lafresnayi

This was the only hummingbird with a markedly decurved bill in the Fonté study area. It is, in fact, the only species with such a bill that occurs at temperate levels anywhere in the Andes. Our feeding records for males and females were very different, and so are treated separately. It is probably significant that females, although shorter-winged, have on average longer bills than males. The mean difference in bill-length is only about 2 mm, but a long-billed female may have a bill 4 mm longer than a short-billed male, and such a difference may well affect their relative efficiency in feeding at different flowers.

Females were recorded feeding mainly at flowers of four species whose long corolla tubes fitted their bills rather closely *(Castilleja, Symbolanthus, Pentadenia* and *Siphocampylus).* Three of these were not seen to be visited 'legitimately' by any other hummingbird species and probably depended on *Lafresnaya* for pollination (see also above, under *Castilleja*). In their behaviour, females seemed to be typical trap-liners, reminiscent of hermit hummingbirds *Phaethornis,* moving between scattered nectar sources and showing no tendency to defend a feeding territory. As mentioned later, a female that regularly visited a large *Castilleja* clump at which a female *Lesbia nuna,* a much smaller bird, held a territory was regularly chased by the latter. They fed silently, but during longer flights between nectar sources regularly uttered a monosyllabic 'seep' (reminiscent of the flight call of some *Phaethornis* species).

Watches at places that females visited on their foraging rounds gave some idea of the timing of their feeding routine. Of 17 intervals between successive visits of what was probably the same bird to a nectar source, 15 were from 10 to 31 min, with a mean of 21 min. This figure is in good agreement with observations made at a feeding site which a female regularly visited, where three of its main food plants *(Castilleja, Symbolanthus* and *Pentadenia)* were flowering close together along the edge of a wooded strip. At each visit it remained in the area for 2 to 11 min, during which it went to a favourite perch between feeding bouts. It would then leave, and was absent for 15 to 38 min.

The rather brief observations suggested that, in contrast to the females, male *Lafresnaya* tend to hold feeding territories. On 22 July, a male held a small territory within a wood in which there were many small *Palicourea* trees in the under-storey and 16 open *Pentadenia* flowers near the ground. This bird was seen feeding only at the *Palicourea.* Feeding bouts were frequent, mostly at intervals of 2–16 min. Once it chased a female *Lafresnaya* which intruded, and once a *Diglossa albilatera.* It was probably present for almost the whole of two watches, totalling 2 h 40 min. It was silent when perched in the territory between bouts of feeding, but it uttered the monosyllabic 'seep' when flying round the territory and between probes when feeding. Another male that was watched for an hour in part of a wood that contained only *Palicourea* and a little *Castilleja* seemed to be attempting to infiltrate a territory previously held by a male *Metallura.* It fed silently, mainly on *Palicourea,* and was occasionally chased by another hummingbird, probably the *Metallura.*

In a place where woodland bordered an area of semi-open bushy second growth, with plants mostly not more than 3 m tall, there was intensive activity on three successive mornings among a group of at least 5 *Lafresnaya.* Watches totalling 5 h were insufficient to clarify the nature of the activity, but it was not related to feeding. One male spent much of the time (at least 77 out of 150 min of one watch) on a small group of perches about 10 m up in a tree on the woodland edge overlooking the bushy area. He was regularly visited at this perch by birds in female plumage and occasionally by male-plumaged birds, and these visits usually led at once to long flight chases over the bushy area in which up to three other birds might join. On the perch the male was silent; flight chases were accompanied by bursts of rapidly repeated calls, 'see-see-see-see . . .', apparently uttered by the bird being chased. This activity suggested an initial stage of some kind of courtship display. Perhaps males group themselves in a 'dispersed lek'; but if so, one would not expect them to be silent on their perches.

Coeligena helianthea

Nearly all our feeding records were of adult males. Females were seen feeding on only two occasions (4 feeding records: *Cavendishia* 2, *Symbolanthus* 1, *Tropaeolum* 1). Males fed predominantly by trap-lining. A few observations suggested that some, at least, spent a good deal of their time at nectar sources that were not within the feeding territories of other hummingbirds, perhaps using them as a base from which to make trap-lining excursions. Aggressive behaviour was seen only once, when a trap-lining male *Coeligena* chased a female *Metallura* that came to a clump of *Passiflora* at the same time as it did. Sixteen intervals between successive visits to the same flowers by what we presumed (from the behaviour) to be the same bird ranged from 16 to 58 min, with an average of 37 min.

Although we had some records of their feeding on small flowers, this fairly large, long-billed hummingbird probably feeds most efficiently from large flowers with straight corolla tubes. At the time of our visit, *Symbolanthus* and *Passiflora* were the only such flowers available. The latter has a corolla tube so long that *Coeligena* cannot probe it legitimately, but instead uses the holes that *Diglossa albilatera* pierces at the base of the calyx. Timed visits of *Coeligena* to *Symbolanthus* flowers lasted from 2 to 9 s, during which up to three probes were made, and visits to *Passiflora* flowers lasted 3–3½ s.

Ensifera ensifera

We saw *Ensifera* feeding only at the flowers of *Passiflora mixta,* and in fact never saw it except when we were watching at clumps of *Passiflora.* The extraordinarily long bill of *Ensifera,* which exceeds in length the head and body combined, closely matches the corolla tube of *Passiflora.* No other plant that was in flower in the study area approached *Passiflora* in the length of the corolla tube.

Ensifera must be a most pronounced trap-liner. Usually a bird suddenly arrived, fed at the *Passiflora* flowers, and flew straight off. Occasionally it perched briefly near the flowers on arrival, or before flying off. Its feeding visits were few and far between. We watched at *Passiflora* clumps for a total of 23 morning hours (0540–1200 h), in which time we saw 6 visits by *Ensifera.* Four other visits were seen in the morning during watches that were not timed (because attention was not being concentrated solely on the *Passiflora*). Although six of the timed watches were longer than 2 h, and two exceeded 4 h, only once did we see two visits by *Ensifera* during a watch (with an interval of 31 min). Nine of the ten visits were in the periods 0600–0800 and 1000–1100 h.

As has been mentioned, practically all the *Passiflora* flowers that were examined had been pierced at the base by *Diglossa albilatera.* In addition, at least four hummingbird species (and at least one butterfly) took nectar from the holes made by *Diglossa.* Visits by the nectar thieves were regular, and the combined visits were frequent. Thus at the main *Passiflora* clump that was studied a male *Diglossa albilatera* made a thorough round of all the flowers about three times per hour, a female *Metallura* about every half-hour, and a male *Coeligena* about every 40 minutes. Doubtless as a consequence of these frequent visits, *Passiflora* flowers that we sampled at this and other clumps yielded very small quantities of nectar; many gave none that was measurable – in spite of the fact that *Passiflora* flowers produce nectar copiously (Table 2).

In order to determine to what extent *Ensifera*'s food supply was being depleted by the nectar thieves, we protected the bases of a number of *Passiflora* flowers by wrapping them with polythene strips while they were still in bud. The experiment was unfortunately terminated prematurely when we had to leave the Fonté area, but the first results were striking. Visits by *Ensifera* to unprotected flowers were brief, 4 being the maximum number of probes that we recorded. On 19 July, 6 days after several flowers had been protected at the clump where most observations were made, an *Ensifera* arrived at the clump, went first to three high, unprotected flowers, probed each of them 2 or 3 times, then flew straight down to one of the wrapped flowers (ignoring several flowers that were nearer), probed it ten times, flew straight to another wrapped flower, probed it 9 times, and then flew off. The two protected flowers had opened 1–2 days previously. Even more striking was a visit by *Ensifera* to the same clump on 22 July. On this occasion it went first to an unprotected flower, fed at it for about 2 seconds, then flew to one of the wrapped flowers (not one of those visited on the 19th, which were now over), made 27 probes, perched briefly, and flew off. It seemed that this bird had learnt which flowers were most rewarding, and that one or two flowers could supply as much nectar as it could take on one visit.

Lesbia nuna

The few males that were seen appeared to be holding territories in open areas with scattered trees, not far from woodland edge. They were mostly seen feeding by making aerial sallies for flying insects from tree perches, and only a single visit was seen to a flower (a low-growing *Rubus*). Many more records were obtained for females, which were seen visiting flowers of five species (Table 3).

Particular attention was paid to one female, which defended a small feeding territory centred on a large clump of *Castilleja*. This bird fed mainly within an area measuring c. 25 by 15 m, containing the *Castilleja* clump and, a little separate, a patch of bushy growth including *Castilleja, Palicourea* and *Cavendishia*. At times it moved out onto an adjacent open field and fed on low *Rubus* bushes, and occasionally it moved about 50 m away to feed on *Palicourea* along a wood-edge. Although it ranged over a 25 × 15 m area for most of its feeding, it defended only the large *Castilleja* clump, not attacking the hummingbirds that often came to feed in the bushy patch about 10 m away. Within the defended area it regularly uttered a short, monosyllabic 'zit, zit' while feeding and immediately after returning to the perch. Between bouts of feeding it perched for much of the time on a few favourite perches close to the *Castilleja* clump. During a 2-hour watch from 0730 to 0930 h it spent 39% of the time on these perches, and during a 2-hour watch from 1345 to 1545 h, 48% of the time.

The only other hummingbird seen feeding at the *Castilleja* clump was a female *Lafresnaya*. Although a considerably larger bird, it was regularly chased by *Lesbia nuna* and on several occasions was either prevented from feeding or had its feeding interrupted. Several timings of feeding rates showed that *Lesbia* was consistently less efficient than *Lafresnaya* in feeding at *Castilleja*. On average *Lesbia* visited a flower every 2·7 s (combined figure from records on 3 days, averaging individually 2·8, 2·3 and 3·1), compared with 1·3 s for *Lafresnaya*. This relative inefficiency seemed to result from the fact that *Lesbia* could not hover and probe the *Castilleja* flowers by inserting its bill along the curvature of the corolla, as *Lafresnaya* could. Instead, it probed the flower either by inserting the bill on the underside, at the point where the corolla tube divides, or by piercing a hole (or using an existing hole) on the upper side of the calyx near the base. Both methods frequently involved clinging to the flower with beating wings.

Chlorostilbon poortmani

This species was seen in only two places, in one of which a male held a feeding territory and was once seen engaged in what appeared to be courtship display with a female. Both were open areas near woodland edge, and the four kinds of plants at which the birds were seen feeding were low-growing herbs or stunted shrubs.

The flower-piercers

Three species of *Diglossa* occurred in the study area, *D. albilatera, D. caerulescens* and *D. carbonaria*. The first two of these occurred mainly in woodland and along woodland edges, while the third was a bird of more open, bushy country. Far the most important of these species, in its effect on the ecology of the hummingbirds, was *D. albilatera*, the smallest of the three and the one whose bill is most highly modified for piercing the base of flowers.

D. albilatera fed very largely on the nectar of *Palicourea angustifolia.* They are small agile birds, and the rate at which they are able to exploit *Palicourea* flowers, about one flower per second, is remarkable. They are regularly attacked by hummingbirds, which clearly recognize them as ecological competitors, and consequently are very furtive, feeding silently and keeping as far as possible to the interior of the plants on which they are feeding.

As already mentioned, the flowers of *Passiflora mixta* were almost invariably pierced by *D. albilatera;* but the proportion of the *D. albilatera* population that fed on *Passiflora* flowers cannot have been very high, as *Passiflora* clumps were sparsely distributed. In contrast to their behaviour at *Palicourea,* they remained for several seconds at *Passiflora* flowers, often piercing them in more than one place, apparently staying until they had extracted all the nectar that they could reach. Although their general behaviour was still furtive, we never saw one attacked while feeding at *Passiflora,* probably because no hummingbirds maintained feeding territories centred on *Passiflora* clumps. The effect of their exploitation of *Passiflora* flowers must have been to reduce greatly the nectar available to *Ensifera,* as discussed above, not only by taking it themselves but also by making available to other hummingbirds a nectar source that would otherwise have been unavailable.

Other flowers seen to be visited by *D. albilatera* were *Cavendishia, Castilleja* and *Symbolanthus* (once each), *Siphocampylus* (twice), a small and apparently rare *Passiflora* lacking a corolla tube, and the introduced foxglove *(Digitalis).* The flowers of *Siphocampylus,* which were just beginning to open when we left the area, are soft and unprotected at the base of the corolla tube, and it seemed likely that their exploitation by *Diglossa* would affect the amount of nectar that they would provide for *Lafresnaya,* their probable main pollinator.

Diglossa caerulescens has a much less specialized bill than *D. albilatera,* and very different habits. Several times we saw single individuals or pairs of *D. caerulescens* accompanying mixed foraging parties of tanagers, flycatchers and other birds. We also saw them eating fruits of *Cavendishia* and *Rubus.* They were recorded visiting flowers of *Palicourea* and *Rubus,* but when they could be observed closely they were seen to enter the flower 'legitimately'. We never definitely saw one piercing a flower.

Diglossa carbonaria, with a bill nearly as specialized as that of *D. albilatera,* was recorded piercing the flowers only of *Palicourea, Cavendishia* and *Manettia.* An individual that held a territory embracing the large *Castilleja* clump at which we spent watches totalling 11 h, showed no interest in the *Castilleja* flowers though it sometimes perched close to them. This species is considerably larger than *D. albilatera* and is not so subordinate to hummingbirds, though its behaviour in approaching and working through vegetation in search of flowers is similarly furtive. Once one was seen to drive an *Eriocnemis vestitus* from a *Cavendishia* flower, and once one was attacked by *E. vestitus* while feeding at *Cavendishia* but was not dislodged.

Observations at Carare

Vegetation, and available nectar sources

Most observations at Carare were made along 1½km of forest path at a height of 2300 to 2450 m. The path ran through an extensive area of forest some 2½ km wide, extending from the ravine of the Rio Uvasa (2000 m) to the top of a steep cliff (Las Alturas, 2800 m) and probably beyond. There had been recent and old selective felling in the forest but apparently no clear felling. In addition observations were made in adjacent open country, some of which was naturally unforested being poorly drained and boggy but most had been cleared and probably regularly burnt. These open areas were at 2200 to 2300 m, with a small area of about 2 ha at 2450 m.

In the forest 20 species of plants and in the open areas 4 species were seen to be visited for nectar by hummingbirds in 10½ days of observation. Of these 24 species, 9 were climbers including the scrambling tree heaths, 7 were woody shrubs, 4 were herbaceous ground-living plants, 3 were trees, and one was an epiphyte (Table 5). Considered by families, the

Table 4 Characteristics of hummingbird flowers, Carare

		Corolla			Nectar	
		length of tube (mm)	colour	orientation[1]	concentration[2] %	production[3] µl
Guttiferae	*Clusia* sp.[4]	nil	cream	U	15–17, 16·0	20 (12 h, night)
Ericaceae	*Cavendishia cordifolia*	15	pink & white	H–P	9–22, 14·9[5]	22 (24 h)
	Cavendishia guatapeenis	10	red	P	19	17·5 (24 h)
	Cavendishia pubescens	31	pink	P	12–21, 16·1	26 (24 h)
	Disterigma sp.[4]	8	white	H	22–41, 27·8	2·5 (24 h)
	Psammisia falcata	29	orange	P	11–18, 14·3	16·2 (8 h, daytime)
	Thibaudia rigidiflora	21	orange-pink	P	13–24, 17·6	9·2 (14 h, night)
Leguminosae	*Phaseolus coccineus*[4]	—	red or white	—	27–45, 35·7	5·0 (5 h, morning)
Melastomataceae	*Huilaea macrocarpa*	(open bell)	red	P	12–16, 13·4	15·5 (2 h)
Gentianaceae	*Macrocarpaea* sp.	(open bell)	cream	P	—	—
Acanthaceae	*Aphelandra* sp.[4]	30	orange	U	24–28, 25·4	5·5 (24 h)
Campanulaceae	*Burmeistera globosa*	30	green	H	10	20 (24 h)
Rubiaceae	*Manettia* aff. *sabiceoides*[4]	11	white	H	25–26, 25·5	3·9 (24 h)
	Palicourea demissa	31	purple-pink	P	14–18, 16·0	46 (24 h)
	Palicourea cf. *vagans*[4]	9	white (calyx yellow)	H	23	3·2 (24 h)
	Palicourea sp. 43[6]	15	yellow (calyx red)	H–P	20–22, 21·0	1·8 (2 h)
	Posoqueria sp.	67	white	H	15–21, 17·0	—
Bromeliaceae	*Guzmania cryptanta*	30	white (bract red & yellow)	U	20–22, 21·0	81 (24 h)
	Pitcairnia sp.	—	white	H	—	—
	Tillandsia aff. *turneri*	36	yellow (bract red)	H–U	18–20, 19·3	98 (24 h)
Amaryllidaceae	*Bomarea* cf. *carderi*	—	pink & green	P	11–17, 13·7	46 (24 h)
Orchidaceae	*Elleanthus smithii*	11	cream & pink	H	8–22, 14·8	7·1 (24 h)

Notes: [1] H = horizontal; P = pendent; U = upright.
[2] range and mean. Single figures indicate single measurements.
[3] amount produced over period indicated in brackets.
[4] also visited by insects.
[5] measurements from Fonté.
[6] collection number; specimen in herbarium of Instituto de Ciencias Naturales, Universidad Nacional, Bogotá.

Ericaceae with 6 species (27% of total nectar records), the Rubiaceae with 5 species (16% of total nectar records) and the Bromeliaceae with 3 species (15% of total nectar records) were making the biggest contribution to hummingbird nectar resources during our visit. Only single members of other families were utilized for nectar.

Herbaceous plants

In the unforested areas two herbaceous ground plants were important and rich sources of nectar: *Guzmania cryptanta,* a bromeliad associated with boggy areas, and an orchid, *Elleanthus smithii,* which grew on dry rocky ground. Both had inflorescent spikes with flowers presented in an upright or horizontal position (Table 4), but the *Guzmania,* with a much longer corolla, produced over ten times more nectar per 24 hours.

At the first visit (31 July to 3 August) the *Guzmania* growing at 2300 m was half over but it was in full flower (average of c. 7 flowers per plant) at 2450 m. Here it grew quite densely, a sample area of c 30 × 20 m containing 139 plants with flowering spikes. By 15 August only 17 of these 139 spikes were still flowering, with a total of only 42 flowers. *Elleanthus* was only just beginning to flower at the first visit but was in full flower at 2200 m between 14 and 21 August. Here it grew extremely densely: an area measuring 1 × 5 m contained 24 flowering spikes and many other equally dense stands were nearby.

The two other open country plants were the ground bromeliad *Pitcairnia,* growing rather sparsely at the edges of bog and forest, and the heath *Cavendishia cordifolia* which grew as a very low shrub (30–60 cm) and was fruiting rather than flowering during our visit. All the remaining 20 species were associated with the forest except the runner bean *Phaseolus coccineus* which was a weed in recent forest clearing.

Trees

The flowering strategies of the three trees were completely different; probably only *Huilaea macrocarpa* has coevolved with hummingbirds. *Posoqueria* sp. is a small under-storey tree 6–10 m tall. Its large, sweet-scented white flowers with long, 67 mm corollas are presumably adapted for pollination by night-flying moths with long probosces. When a small tree was cut down at 1340 h in order to examine the flowers, four anthers pressed together blocked the entrance to the tubular corollas but these anthers sprang open when pushed by a pipette. *Posoqueria* flowers were only visited by hummingbirds early in the morning, the short-billed species obtaining their nectar through pierce holes at the base of the corolla.

Clusia grew in patches of secondary forest, reaching a height of 8–12 m. Trees in full flower bear masses of abundantly staminate, cream-coloured flowers, whose corollas are open shallow cups. Individual flowers open early in the morning and are over by evening. On opening, flowers were found to contain an average of c. 20 µl of nectar. Many insects and different species of hummingbirds visited the *Clusia* flowers, particularly in the early morning.

Huilaea was a common under-storey tree growing to a height of 14 m. Seven trees examined showed all stages of flowering and fruiting on each tree, and it looked as if the species might have a continuous flowering regime throughout the year or at least for the greater part of the year. The flowers are large, open, pendent red bells; the pedicel is long and the calyx is a hard woody hemisphere. Flowers *in situ* were too high to be reached; but three obtained by cutting down the limb of a small tree contained 9·5–22 µl (average 16·5 µl) of nectar. One, bagged at 11·00 h, contained 15·5 µl of 13% nectar 2 h later. Individuals of *Boissoneaua flavescens* were territorial at all the *Huilaea* trees that were watched. No insects or flower-piercers were seen to visit the flowers.

The following characteristics of *Huilaea* indicate that it is adapted for hummingbird pollination: the large pendent red flowers (p. 134) with copious nectar of low sugar concentration (p. 137), the woody calyx (protecting the nectaries from nectar-thieves – p. 134), and the long flowering season (which ensures a long-term nectar supply for a reliable, long-lived pollinator). It is noteworthy that *Huilaea* is a monotypic genus known only from the

Colombian Andes, and belongs to a family (Melastomataceae) whose species are typically insect-pollinated.

The Ericaceae

The Ericaceae showed examples of different flowering strategies, both for attracting pollinators and for avoiding flower-piercers. Within the forest the abundant *Disterigma* sp., a shrub up to 2 m in height, was flowering plentifully at both visits. Its many small white flowers are evenly scattered all over the densely growing shrub; the flowers are presented horizontally and produce small amounts of concentrated nectar (Table 4). It is much visited by bees, which are presumably its pollinators. Although short-billed hummingbirds, particularly the very small *Adelomyia,* fed at it, this heath appears not to have evolved away from the hymenopterophilous syndrome. *D. albilatera* was once seen at it, but only 2 out of 25 flowers examined had pierce holes. Presumably such dispersed, small amounts of nectar, also available to insects, are not an attractive food source for flower-piercers.

No insects were seen to visit the two scrambling tree heaths *Psammisia falcata* and *Thibaudia rigidiflora.* Both have pendent bright pink or orange flowers with long corollas which bloom in dense ranks along horizontal woody stems or twigs. The corollas are unprotected and 71% of 58 flowers of *P. falcata* and all of 10 *T. rigidiflora* flowers examined had been pierced at the base. *D. albilatera* was frequently observed piercing the corollas of both plants. These two heaths appeared to have different flowering seasons, a characteristic of related ornithophilous plants (Stiles 1975, 1978). Thus *P. falcata* was in full flower at the lowest forest levels (2350 m) during both visits but not flowering at higher levels, while *T. rigidiflora* was not flowering inside the forest at either visit but at the second visit a few flowers were out at the forest edge at 2350 m and an isolated bush in cleared land at c. 2250 was in full flower. *Psammisia* was an important source of nectar for *C. prunellei* and *Doryfera,* and the former was also seen to feed at *Thibaudia.* A characteristic of these heaths is the dense packing of stamens, particularly in *Psammisia,* so that in the latter it requires some pressure to push a micropipette more than 19 mm down the corolla tube. Possibly this serves to exclude all but a few hummingbird species, and so increases the likelihood of outcross pollination.

The three *Cavendishia* species present their flowers clustered together in groups of from 5 to 13 flowers, with the base of the corollas enclosed by several layers of leaf-like bracts. In *C. pubescens* the bracts are thick and densely covered with hairs, the clusters are pendent and the corollas long (31 mm). This species was an important nectar source for *Doryfera* and *Coeligena torquata,* both long-billed trap-lining hummingbirds. Only one out of 13 flowers examined had a pierce hole in the corolla and no flower-piercers were seen feeding at them.

C. guatapeensis had nearly finished flowering at the time of our visit, so observations were few. Its flower clusters are pendent and the corollas short (10 mm); they were not examined for pierce holes. Both long- and short-billed hummingbirds were seen to feed at them, but no insects were noted.

C. cordifolia was found only as a low-growing shrub on cleared rough land and on the forest fringes; it was mainly fruiting at the time of our visit and had few flowers. *C. cordifolia* flowers have shorter bracts than *C. pubescens* and the corolla tubes are readily pierced by *Diglossa albilatera;* only a small number were examined but all were pierced. The flowers are orientated between horizontal and pendent, and the corolla tube averages 15 mm in length. At Carare two short-billed hummingbirds were seen to feed at it; at Fonté all the hummingbirds except *Ensifera* fed at it.

While all three *Cavendishia* species are visited and probably pollinated by hummingbirds, *C. pubescens* shows the most advanced adaptations for hummingbird pollination, i.e. the highest nectar production per flower, restriction of nectar to long-billed hummingbirds (indicating coevolution with specialist pollinators – see p. 134), and adequate protection of the nectar from flower-piercers.

The Rubiaceae

Hummingbirds visited five species of Rubiaceae, one of which *(Posoqueria)* has already been described. Two species, *Manettia* aff. *sabiceoides* and *Palicourea* cf. *vagans*, were visited by bees as well as by hummingbirds. Both have features typical of bee-pollinated flowers: white corollas 9–10 mm long presented horizontally, each flower containing a small volume of nectar of relatively high concentration (23–25·5%). The *Manettia*, which also grew at subtropical altitudes at Togui, has no ornithophilous features. The small white flowers with green calyces are scattered evenly all over the plant. Only two very small hummingbirds were seen feeding at it, *Ocreatus underwoodi* at Carare and *Chlorostilbon gibsoni* at Togui. Both were only seen to feed early in the morning and there was good evidence that *C. gibsoni* stopped feeding when bees became active and began to feed at it (see p. 133). *Palicourea* cf. *vagans* shows some ornithophilous characters: the flowers are visually more conspicuous as the calyx is yellow, and they grow in a loose panicle. Spatial concentration of the flowers probably makes them less energetically costly for a hummingbird to exploit. This *Palicourea* was an extremely common small shrub and seven species of hummingbird were seen to feed at it at various times of day; 82% of nectar records were from species with beak lengths of 18 mm or less.

The two remaining species of Rubiaceae, both *Palicourea*, show many more ornithophilous characters. *Palicourea* sp. 43 was a large shrub or small tree growing to a height of 5 m. The flowers are borne in loose panicles, orientated between horizontal and pendent. The tubular corolla is yellow, averaging 15·4 mm in length, and the calyx is red. The nectar could only be sampled by cutting down a small limb. If the nectar secretion which accumulated 2 hours after the limb was cut is typical (Table 4), the quantity per flower is high. Two shrubs formed the feeding territory of a male *Heliangelus*. During watches totalling 3 h on two mornings it fed almost exclusively at these shrubs and drove off a *Diglossa albilatera* which attempted to feed at them.

Palicourea demissa shows the most advanced ornithophilous characteristics. The purple flowers, borne in groups, have long pendent tubular corollas and abundant nectar of low concentration. The corolla is thick and fleshy, probably for the protection of the nectar from flower-piercers, which were not seen to visit the flowers in 4 h of watching. *P. demissa* is a woody scrambler and was found flowering as low as 1 m in disturbed forest and at 10 m in undisturbed forest. Many of these characteristics suggest convergence with tree-heaths such as *Psammisia* and *Thibaudia*, and in fact they share the same *Coeligena* pollinators (Table 5). There was good evidence that short-billed hummingbird species such as *Adelomyia*, *Boissoneaua* and *Heliangelus* did not visit *P. demissa*, nor was it visited by insects.

Other plants

Of the remaining plants, three climbers and two shrubs, only one appeared to be adapted for hummingbird pollination, the climber *Bomarea* cf. *carderi*. This was abundant and in flower at 2350 m, and was also flowering but less abundant at higher levels. The inflorescence is a cluster of pendent flowers with long pedicels. Each flower is tripetalous, with nectaries at the base of each petal. The nectar is abundant and of low concentration. The basal portion of the petal is rolled up and joined to form a long thin tube, which is so narrow that it is impossible to insert a fine pipette (c. 0·6 mm external diameter) into it. The nectar is thus available only to hummingbirds with long thin bills that can hover and exert some upwards thrust, an ability similar to that needed for feeding at the heath *Psammisia*. Only *Coeligena torquata* was seen to feed at it. *C. prunellei*, a thicker-billed bird, is probably unable to reach the nectar as it was frequently seen to fly past and ignore it.

Aphelandra sp., a climber with conspicuous orange flowers, was visited by large bees as well as by hummingbirds, and may be primarily bee-pollinated. It has the following characteristics associated with bee rather than hummingbird pollination: flowers pointing more or less upwards; tubular corolla enlarging at the mouth, with a lower landing lip; and small quantities (5·5 μl) of high concentration (25%) nectar. In spite of its long corolla its nectar is available to such short-billed hummingbirds as *Adelomyia*, *Heliangelus* and

Aglaiocercus, probably because the wide end of the corolla enables these species to insert part of their heads into the mouth of the flower.

Feeding ecology of the hummingbirds

Of the 12 species of hummingbirds recorded at Carare, all but two were resident and seen every day that watches were kept on appropriate flowers. The two exceptions were *Acestrura mulsant,* which was seen on four occasions between 1 and 3 August but not at all between 14 and 21 August, and *Aglaiocercus kingi,* which was seen on only three of the possible $10\frac{1}{2}$ days of observation.

Nine of the 10 regular species can be subdivided into four groups: two small forest species with short bills and wings, *Adelomyia melanogenys* and *Ocreatus underwoodi,* most of whose nectar flowers had short corollas and were also visited by insects, mainly Hymenoptera; two behaviourally similar forest species with long wings and short bills, *Boissoneaua flavescens* and *Heliangelus amethysticollis,* which combined territoriality over concentrated nectar resources with a high percentage of insect-feeding by hawking; three long-billed woodland species, *Coeligena prunellei, C. torquata* and *Doryfera ludoviciae,* all of which were trap-liners, largely feeding on specialized hummingbird flowers; and two non-woodland species, *Colibri coruscans* and *Chlorostilbon poortmani,* only seen feeding in open areas. The tenth species, *Colibri thalassinus*, was seldom seen feeding, although a total of seven individuals with tree-top song posts along forest-edges were regularly present and sang throughout the day. The few feeding records were from forest openings or edges.

The feeding records for hummingbirds at Carare are summarized in Table 5.

Adelomyia melanogenys
Ocreatus underwoodi

Both species were confined to the forest. *Adelomyia* was probably the most abundant forest hummingbird; *Ocreatus* appeared to be considerably less abundant, as indicated by the number of feeding records (Table 5), but the difference may be due in part to the height at which if fed, 4–7 m (mean 3·2) compared with 0·6–7 m (mean 1·4) in *Adelomyia,* as small hummingbirds feeding high up, especially in the crowns of trees, are difficult to see. *Ocreatus* was also seen hawking for insects at a height of 10 m.

Eighty-three per cent of the nectar records for *Adelomyia* were from flowers at which insects, mostly Hymenoptera, also fed (the probably night-flowering *Posoqueria,* which it exploited through pierce-holes, is excluded). The seven flowers with tubular corollas that it visited had effective corolla lengths of 8–30 mm, (mean 14·2), and none of them were pendent. *Adelomyia* was not basically territorial but appeared to be trap-lining over considerable distances, mainly to flowers with small amounts of nectar (e.g. *Disterigma*) which would be uneconomic for the larger trap-lining hummingbirds to visit, or to plants where the amount of nectar per flower was higher but only a few flowers were blooming per plant (e.g. *Palicourea* sp. 43). Timed intervals between return visits to the same flower were 13 min for *Aphelandra* and 26 min for *Palicourea* cf. *vagans.* The times spent at each flower were generally extremely short. Territorial behaviour (calling while feeding) was noted only from a bird feeding in a small forest clearing at *Phaseolus* flowers that were also being visited by *Chlorostilbon poortmani,* and from a bird feeding in the early morning at the pierce holes of *Posoqueria* flowers in company with conspecifics and *Ocreatus.* An *Adelomyia* was repeatedly driven away from profusely flowering *Palicourea* sp. 43 by a territorial *Heliangelus.*

Three out of the four flower species visited by *Ocreatus* (omitting *Posoqueria,* which it exploited through pierce holes) were also visited by insects. *Ocreatus* visited flowers with short corolla tubes that were not pendent (effective corolla lengths 9–15 mm, mean 11·7) and open cup flowers such as *Clusia* sp. It was only seen visiting *Clusia,* where there was much territorial activity between many large hummingbirds, after the early morning peak of feeding activity. The only encounters seen were with conspecifics at *Clusia,* and when it was chased by *Adelomyia* at *Posoqueria.*

Boissonneaua flavescens
Heliangelus amethysticollis

These two species have short bills in relation to their wing-lengths, especially *Boissonneaua* whose bill is only 23% of its wing-length (Table 1). As discussed later (p. 136), this is characteristic of territorial species, and it may also be associated with efficiency in hawking for insects, a method of feeding that was important for both species.

Boissonneaua and *Heliangelus* were to a large extent separated by the height at which they fed. The average height of the 56 nectar-feeding records for *Boissonneaua* was 8·1 m (range 3–12 m), and that of the 34 records for *Heliangelus* 2·8 m (range 0·6–6 m). These height differences were mainly due to the fact that the feeding territories of *Boissonneaua* were based on *Huilaea* trees, whose flowers were mainly at 6–12 m, whereas one of the two feeding territories of *Heliangelus* was based on a patch of ground bromeliads *(Guzmania cryptanta)* and the other on shrubs of *Palicourea* sp. 43, whose flowers were at 1·5–5 m. The heights at which they hawked for insects differed in the same way, *Boissonneaua* usually making long sallies of up to several metres from high perches (mean perch height for 96 sallies 8·6 m, range 2–14 m) while *Heliangelus* made short sallies of 1 m or less from low perches (mean perch height for 20 sallies 2·8 m, range 2·5–3 m).

Boissonneaua and *Heliangelus* have in common two behavioural characteristics associated with territorial defence. One is to hold both wings open and vertical above the back for about half a second after landing. Thus a *Boissonneaua,* after an encounter with a conspecific, fed at five *Huilaea* flowers on one tree, perching briefly with wing display after each feed. When no encounter had taken place for the previous 40 min, a *Boissonneaua* perched four times with wing display during a feeding bout lasting 1 min 9 s, during which 21 *Huilaea* flowers were visited. In a typical instance a male *Heliangelus,* 8 min after chasing an *Adelomyia* from its feeding territory, perched briefly with wing display eight times during a feeding bout at a single bush of *Palicourea* sp. 43 lasting 1 min 39 s. Secondly, both species periodically circle part of their feeding territory in level flight uttering a trilling call. These circular flights were made at heights of 4–6 m by *Boissonneaua* and about 3 m by *Heliangelus.*

Boissonneaua fed mainly at mid to canopy levels in the forest, including the canopy-flowering *Clusias* that grew in places along the forest edge. As well as conspecifics, it was seen to drive *Heliangelus, Colibri coruscans* and *Chlorostilbon poortmani* from its feeding territories. It failed to drive off a *Coeligena prunellei* (from *Huilaea*) but made vigorous attempts to do so.

The four flowers with tubular corollas which it visited had effective corolla lengths of 8–15 mm (mean 10·7). Three out of the seven flower species which it visited were also visited by insects, but these three accounted for only 29% of nectar records. During our visit the under-storey tree *Huilaea macrocarpa* was undoubtedly its most important source of nectar (66% of all nectar records). Eight different *Huilaea* trees found flowering in four different areas were all centres of *Boissonneaua* feeding territories and except for one record for *Coeligena prunellei* no other hummingbirds were seen feeding at them in a total of 5 h of watching.

Some individual *Boissonneaua,* apparently with compact territories, continually uttered a repeated *sip sip,* at an average rate of 30 *sips* per minute, when in their territories except while they were on the wing nectar-feeding or hawking for insects. One such individual, watched for 1 h on a sunny but rather windy afternoon, called for 91% of the time. For the remainder of the time, except for 1 min 34 s when it was not in view, it made 9 hawking sallies and 10 visits for nectar to a total of 13 *Huilaea,* 9 *Disterigma* and 8 *Palicourea* cf. *vagans* flowers. Another 1 h afternoon watch on the same individual, when the weather was overcast and still in the first half of the watch and slightly breezy in the second half, gave the following results: first $\frac{1}{2}$ h, 41 insect-hawking sallies and 4 nectar visits to a total of 5 *Huilaea* flowers, average interval between visits 8·7 min; second $\frac{1}{2}$h, 33 insect-hawking sallies and 5 nectar visits to a total of 10 *Huilaea* flowers, average interval between nectar visits 5·8 min. It was evident that the still overcast weather was the more suitable for insect hawking and an indication that even a slight breeze may decrease the profitability of such an activity. The

Table 5 Hummingbird feeding records, Carare

	D.l.	*C.th.*	*C.c.*	*C.po.*	*A.me.*	*C.pr.*	*C.to.*	*B.f.*	*H.a.*	*O.u.*	*A.k.*	*A.mu.*
Herbaceous plants, ground												
Guzmania cryptanta		6	19	11					8			1
Pitcairnia sp.			2									
Elleanthus smithii			19	2	3							
Herbaceous plants, epiphytic												
Tillandsia aff. *turneri*						9						
Vines/climbers												
Cavendishia pubescens	5						8					
Psammisia falcata	14					28					1[1]	
Thibaudia rigidiflora						1						
Phaseolus coccineus				4	15							
Aphelandra sp.					2	5			1		2	
Manettia aff. *sabiceoides*										2		
Palicourea demissa						11	1					
Bomarea cf. *carderi*							3					

Table 5 Hummingbird feeding records, Carare (cont.)

	D.l.	*C.th.*	*C.c.*	*C.po.*	*A.me.*	*C.pr.*	*C.to.*	*B.f.*	*H.a.*	*O.u.*	*A.k.*	*A.mu.*
Woody shrubs												
Cavendishia cordifolia				1	1							
Cavendishia guatapeensis					2		1	1				
Disterigma sp.					11			4	4			
Macrocarpaea sp.						5	1					
Burmeistera globosa						1						
Palicourea cf. *vagans*					6	2	2	5	3	3		1
Palicourea sp. 43	2				1	1	1	2	13	1		
Trees												
Clusia sp.		19	12		1			7	5	2	1	
Huilaea macrocarpa						1		37				
Posoqueria sp.					5[1]	1				1[1]		
Other plants					2							
Insect-hawking		2	1			3	1	96	20	1		1
Insect-gleaning				1		1	1	1				
Totals (481)	21	27	53	19	49	69	19	153	54	10	4	3

Hummingbirds abbreviated as follows: *A.k., Aglaiocercus kingi; A.me., Adelomyia melanogenys; A.mu. Acestrura mulsant; B.f., Boissoneaua flavescens; C.c., Colibri coruscans; C.po., Chlorostilbon poortmani; C.pr., Coeligena prunellei; C.th., Colibri thalassinus; C.to., Coeligena torquata; D.l., Doryfera ludoviciae; H.a., Heliangelus amethysticollis; O.u., Ocreatus underwoodi.*

Note: [1] nectar taken 'illegitimately', through pierce holes.

lack of records on the second afternoon from *Disterigma* and *Palicourea* cf. *vagans*, with their small nectar rewards compared to *Huilaea* (Table 4), suggests that they may be visited only when there is insufficient food available from other sources.

Heliangelus is an aggressive territorial species of forest and forest edge. In two morning watches totalling 2 h 50 min a male with a territory centred on two *Palicourea* sp. 43, drove off *Adelomyia* seven times, *Coeligena torquata* twice, and a *Doryfera* and *Diglossa albilatera* once each, all of which were attempting to feed at the *Palicourea*. It was unable to keep *Boissoneaua* from the *Palicourea* although it persistently attempted to.

During an 80-min morning watch this male spent 9% of the time feeding, 4% chasing intruders, and 61% perched in the territory; the remainder of the time it was out of view. During another 90-min morning watch it spent 11% of the time feeding, all but 30 s at *Palicourea* sp. 43 (corolla length 15 mm). During these watches *Heliangelus* never visited two profusely flowering plants of *Palicourea demissa* (corolla 31 mm) which were only 2–3 m from its main perch in *Palicourea* sp. 43. During a 40-min watch where *Cavendishia* cf. *pubescens*, *Palicourea* cf. *vagans* and *Disterigma* sp. were growing close together and could be simultaneously watched, *Heliangelus* came twice to visit the *Palicourea* and *Disterigma* (corollas 9 and 8 mm), by-passing the *Cavendishia* (corolla 31 mm). It is probably not just its short bill which prevents *Heliangelus* from feeding at such flowers as *P. demissa* and *C.* cf. *pubescens*, as one held a feeding territory over a group of the ground bromeliad *Guzmania* whose flowers have long corollas (30 mm) but grow at an angle between upright and horizontal. Probably the pendent growth of the former two flowers is the main factor preventing *Heliangelus* from feeding at them.

Coeligena prunellei

Of the three long-billed trap-liners, *C. prunellei* was the most abundant and was seen to visit the greatest number of different flower species. It is the largest in wing length and weight (Table 1), but compared with the other two species in this group its bill averages 3 mm shorter, and is appreciably stouter.

Seventy per cent of the nectar records for this species were from vines or climbers, including the climbing tree heaths (i.e. *Psammisia falcata, Thibaudia rigidiflora, Palicourea demissa* and *Aphelandra* sp.), all of which were flowering in undisturbed forest near canopy level and at much lower levels in disturbed forest and clearings. *C. prunellei* visited these flowers at both levels. The bromeliad *Tillandsia* aff. *turneri*, to which only *prunellei* was seen to go, was epiphytic on trees at heights of 5–12 m (mid to lower canopy levels).

C. prunellei fed mainly by trap-lining. Mean intervals between successive visits to the same flowers were as follows: at profusely flowering *Psammisia* 23 min; at *Palicourea demissa* 40 min; and at well-spaced single plants of *Tillandsia* 44 min. In places where selective felling had greatly increased the growth and flowering of such heaths as *Psammisia falcata* and so provided a concentrated nectar source, it occasionally perched nearby and showed territorial activity, chasing off *Doryfera* (5 chases in 3½ hours watching) which was the only other species seen feeding at this flower. Out of a total of 47 feeding records it was silent while feeding except on four occasions when it uttered a monosyllabic 'ick' between probes. Typically, calling while feeding is characteristic of territoriality; its infrequency in *prunellei* suggests that this is not a common strategy. Although competition with its congener *C. torquata* might have been expected, only one encounter was seen when *prunellei* chased *torquata* from the vicinity of *Palicourea demissa.* Results of encounters between the two *Coeligenas* and other species of hummingbird suggest that *torquata* is always subordinate to the slightly larger *prunellei.* The lack of encounters observed between them was due to the fact that no nectar feeding was recorded for *prunellei* above c. 2400 m, whereas all but two of the records for *torquata* were above this level. The heath *Psammisia* was abundant and in full flower at 2350 m; at higher levels it was present but the flowers were not open. As *Psammisia* appeared to be the most important nectar source for *prunellei,* this was probably the underlying reason for the partial altitudinal separation of the two *Coeligenas.*

Except for three records of *prunellei* visiting the two *Palicoureas* with short corolla tubes (9 and 15 mm), the seven plants with tubular corollas which it visited have long corolla lengths, (21–67 mm, mean 34·9). Seventy-two per cent of all nectar records were from plants whose flowers are pendent so that the hummingbird needs to hover upwards into them. In addition the flowers of two of the heaths are so full of stamens as to require considerable upward pressure to penetrate them. The following evidence suggests that other hummingbirds are unable to utilize these heaths. In 11 hours of watching at six different plants of *Psammisia* only *prunellei* and *Doryfera* came for nectar except for one visit to pierce holes by *Aglaiocercus kingi.* During 3½ hours of watching at various times of day at a profusely flowering bush of *Thibaudia* left by clearance c. 200 m from the nearest woodland, only *Diglossa* fed at its nectar although the two open country hummingbirds *C. poortmani* and *C. coruscans* were both seen perching on it at different times. On the other hand *prunellei* seemed to be unable to exploit the flowers of *Bomarea* cf. *carderi,* which were an important nectar source for the slender-billed *C. torquata* (see below). In the course of 3 h of watching at a place where *B.* cf. *carderi* and *Palicourea demissa* could be watched simultaneously, *prunellei* went six times to the *Palicourea* but did not visit the *Bomarea.*

Coeligena torquata

C. torquata, the longest-billed of the Carare hummingbirds, was a silent, trap-lining nectar feeder confined to the forest, where it was recorded feeding at heights of 1–12 m (mean 5·2 m). It was chased by *C. prunellei* and *Heliangelus,* and was seen to be aggressive only to conspecifics. Records were few and it appeared not to be so abundant as *C. prunellei,* particularly at lower elevations. Like the latter it largely (76% of all records) went to pendent flowers with long corolla tubes at which insects were not recorded. On occasions when *Palicourea* cf. *vagans,* with a short corolla, and *Cavendishia* cf. *pubescens,* with a long corolla, could be watched simultaneously, in a total of 2½ h it entirely ignored the *Palicourea* and went only to the *Cavendishia.* This was the only species seen feeding at *Bomarea* cf. *carderi,* a flower that was avoided by *C. prunellei* (see above).

Doryfera ludoviciae

This species was a pronounced trap-liner, showing no evidence of territorial behaviour. Adults were mainly seen foraging at the heaths with long pendent corollas; their extremely fine pointed bills are probably well fitted for probing this kind of flower, which they exploited at the rate of 0·8 s (*Cavendishia* cf. *pubescens*) and 0·9 s *(Psammisia)* per flower (cf. 1·4 s per flower for *C. prunellei* at *Psammisia*). They were frequently seen to be dominated by *C. prunellei* and occasionally by *Heliangelus.*

Feeding records for two juveniles which were still being fed by a parent are omitted from Table 5. For 10 days these two juveniles were sedentary in a small area of thick undergrowth measuring about 10 by 4 m, where they supplemented parental feeds by feeding at *Disterigma* (16 records) and *Cavendishia guatapeensis* (3 records). They were also seen hawking for insects three times. They appeared to drive *Adelomyia* from the *Disterigma* in this area, but possibly the apparent attacks were mistaken food-begging.

Colibri coruscans

C. coruscans was only seen in open areas where it was highly territorial and vocal. At our first visit to Carare (31 July to 3 August) all the *coruscans* feeding territories were centred on the ground bromeliad *Guzmania cryptanta,* which was then probably at its peak of flowering. By 15 August only 12% of the *Guzmania* were still flowering and no *coruscans* held territories over them, but some were singing and holding feeding territories over the orchid *Elleanthus smithii,* mostly at 2200 m where it was flowering profusely in dense stands. Among the extensive boggy areas at 2450 m where the *Guzmania* grew, were wooded islands with *Clusia* trees which were flowering at both visits. At the first visit *coruscans* was frequently foraging at these *Clusias,* which appeared to form part of their feeding territories. At the second visit when the *Guzmania* was largely over, visits by *coruscans* to *Clusia* were intermittent and they were not singing in the area. Territorial *coruscans* sing almost continually and frequently call between probes while feeding. Most encounters were between conspecifics, but they were also seen chasing *C. thalassinus* from *Clusia* and were themselves driven from this tree by *Boissoneaua.*

They frequently perch while feeding at *Guzmania* and *Elleanthus* and occasionally do so at *Clusia.* It is probably of significance that the four plant species at which *coruscans* foraged present their flowers either in an upright or horizontal position (Table 4); no feeding was recorded at pendent flowers.

The smaller *Colibri thalassinus* was seen foraging at two plants, *Guzmania* and *Clusia.* The *Guzmanias* at which it was seen to feed were either in small forest openings or close to the forest edge; it was never seen feeding well out in cleared areas, as was *coruscans. C. thalassinus* was recorded feeding at *Clusia* in the second period of observations, when most of the *coruscans* had descended to lower elevations to hold territories at the *Elleanthus.* It appeared to be more sedentary than *coruscans,* and seven singing males occupied the same song posts throughout both periods of observation.

Chlorostilbon poortmani

C. poortmani was common in open areas, where it fed at *Guzmania* and *Elleanthus* flowers. When *Guzmania* was largely over and abandoned by *Colibri coruscans, poortmani* continued to feed at the sparse flowers. It also fed in recent forest clearings on the bean *Phaseolus.* It foraged at heights of 0·6–4 m (mean 1·1 m) and often called in flight between nectar sources, but not while feeding. Except for a record at *Cavendishia cordifolia* it fed at flowers whose corollas were orientated between horizontal and upright. *C. poortmani* was not seen engaging in territorial encounters, but behaved as a trap-liner of scattered resources in unforested country.

Observation at Togui

Vegetation, and available nectar sources

The impoverished flora of the hacienda near Togui included 11 plant species which were providing nectar for hummingbirds at the time of our visit (Table 6, which also includes two other plant species found in cultivated country beyond the bounds of the hacienda). Far the most conspicuous was the introduced tree *Eugenia jambos,* which grew mainly along river banks and in hedges between pastures. Introduced plants *(Eugenia, Musa* (banana), *Ipomoea* sp. and *Canna indica)* accounted for 77% of all records of nectar feeding.

Eugenia jambos, with its copious nectar of low concentration, was the main nectar source for all the hummingbird species except for *Phaethornis guy* and *Chlorostilbon gibsoni,* which were not recorded at it. Many species of butterflies and other insects also fed at it. Butterflies were observed feeding between 0822 and 1521 h, bees between 0720 and 1615 h. Nectar rewards for hummingbirds must have been highest in the early morning and late evening; they were recorded feeding at *Eugenia* between 0605 and 1806 h, with peaks in the morning and evening.

Guzmania sp., an epiphytic bromeliad, grew high in the trees with its 1·5 m inflorescence stem often reaching up into the crown. It was abundant, but only one plant was found with flowers, which were visited by *Amazilia cyanifrons,* apparently the most pronounced aboreal feeder of the hummingbirds present. Small bees go to the rim of the tubular corolla of this *Guzmania* but do not enter it. Individual flowers last less than 24 h and produce nectar with an average concentration of 17·8%, a typical figure for hummingbird-pollinated flowers. The four other plants with mean nectar concentrations between 14 and 19% (Table 6) also have visual or morphological characters typical of hummingbird flowers, i.e. pink, red or orange colours in or near the inflorescence (all species), and tubular corollas which are pendent or

Table 6 Characteristics of hummingbird flowers, Togui

			Corolla		Nectar	
		Length of tube (mm)	colour	orientation[1]	concentration[2] %	production[3] µl
Ericaceae	*Cavendishia pubescens*[4]	19	pink	H–P	15–20, 17·7	—
	Psammisia penduliflora	15	red	P	10–18, 15·0	2·0 (18 h)
Leguminosae	*Calliandra purdiei*	nil	pink & white	U	—	—
Myrtaceae	*Eugenia jambos*[5]	nil	cream	U	6–17, 9·7	47 (24 h)
Apocynaceae	*Mandevilla* aff. *mollissima*[5]	25	green & white	H	—	—
Convolvulaceae	*Ipomoea* sp.[5]	—	pale pink	H	16–46, 37·8	13·3 (12 h)
Scrophulariaceae	*Castilleja communis*	7	green (flag red)	H–U	11–27, 18·8	1·5 (24 h)
Rubiaceae	*Hamelia patens*[5]	18	orange	H–P	11–20, 14·8	7·9 (24 h)
	Manettia aff. *sabiceoides*[5]	11	white	H	25–26, 25·5	3·9 (24 h)
Bromeliaceae	*Guzmania* sp.	15	purple & red	H–U	14–19, 17·8	11·9 (18 h)
Musaceae	*Musa* sp.	35	green	H–U	9–16, 13·0	84 (18 h)
Strelitziaceae	*Heliconia* sp.	30	yellow & red	H	—	—
Cannaceae	*Canna indica*	25	red	H–U	6–11, 7·3	29 (24 h)

Notes: [1] H = horizontal; P = pendent; U = upright.

[2] range and mean.

[3] means for day (24 h) or part of day.

[4] collection no. 49 (I.C.N. Herbarium); distinct from *C. pubescens* at Carare (Table 4).

[5] also visited by insects (*Ipomoea* and *Manettia* by Hymenoptera; *Mandevilla* and *Hamelia* by Lepidoptera; *Eugenia* by various insects).

partially so (all except *Castilleja*). *Castilleja communis* differs from the others in having hidden closed green flowers beneath a rosette of red leaves.

Of these five native species, which are probably hummingbird-pollinated, only *Psammisia* cf. *penduliflora* was seen to have its corolla slit by nectar-thieving Bananaquits *Coereba flaveola,* which at Togui took the place of the flower-piercers (*Diglossa* spp.). There was evidence that such plundering was reduced by hummingbird territoriality. Thus 43% of the 28 flowers examined were slit in two small separate groups of 16 and 22 flowers, which were not defended by a hummingbird; but in a large plant with c. 300 flowers within the territory of an *Amazilia tzacatl,* none of 22 flowers examined were slit in this way.

Table 7 - Hummingbird feeding records, Togui

	P.g.	*A.n.*	*A.f.*	*A.c.*	*A.t.*	*C.g.*
Herbaceous plants, ground						
Castilleja communis						1
Musa sp. (banana)	6	17	11		1[1]	
Heliconia sp.	1					
Canna indica	2		9		1[1]	
Herbaceous plants, epiphytic						
Guzmania sp.				5		
Climbers						
Psammisia penduliflora			2		5	
Mandevilla aff. *mollissima*						2
Ipomoea sp.					2	3
Manettia aff. *sabiceoides*						10
Shrubs						
Cavendishia pubescens			6		7	
Hamelia patens			3	1	4	14
Trees						
Calliandra purdiei					5	
Eugenia jambos		9	27	38	67	
Insect-hawking		19	23	20	34	
Insect-gleaning	1	2		1	9	
Totals (368)	10	47	81	65	135	30

Hummingbirds abbreviated as follows: *A.c., Amazilia cyanifrons; A.f., Amazilia franciae; A.n., Anthracothorax nigricollis; A.t., Amazilia tzacatl; C.g. Chlorostilbon gibsoni; P.g., Phaethornis guy.*

Note: [1] nectar taken 'illegitimately', through pierce holes.

Feeding ecology of the hummingbirds

Six hummingbird species were resident on the hacienda at the time of our visit (Table 7), of which four *(A. tzacatl, A. cyanifrons, C. gibsoni, P. guy)* were seen nest-building. Two other species *(A. melanogenys, A. mulsant)* were each seen once. In spite of the degradation of the indigenous flora and the predominance of introduced plants, the six resident hummingbirds largely occupied different feeding niches.

The three *Amazilias* consisted of two territorial species *(A. tzacatl, A. cyanifrons)* and a non-territorial trap-liner *(A. franciae).* The main difference in their feeding ecologies is in accordance with their relative bill-lengths, as measured by the bill/wing index (for further discussion see p. 136). In weight and wing-length the three species are similar (Table 1), but *franciae* has a considerably longer bill (bill/wing 45%, cf. 33% in *cyanifrons* and 37% in *tzacatl*). *A. franciae* fed at all levels, from herbaceous plants at 0·5 m to the tree canopy. At *Eugenia* trees it was dominated by the two other *Amazilia* spp., and consequently fed frequently at small, undefended trees with few flowers. The greatest amount of overlap was found in the feeding niches of *A. tzacatl* and *A. cyanifrons,* both of which held feeding territories at *Eugenia* trees. *A. cyanifrons,* however, tended to keep to higher levels and exploited a more limited range of plant species.

Anthracothorax nigricollis was territorial over high insect-hawking perches; a considerably larger bird than the *Amazilias,* it was able to feed unmolested at the ubiquitous *Eugenia* but did not defend its nectar. *Phaethornis guy* was a trap-line feeder on herbaceous plants with long corollas. *Chlorostilbon gibsoni* was also a trap-liner, feeding at low-growing flowers of herbs, shrubs and vines with short corollas, most of its nectar being shared with insects.

Amazilia tzacatl

A. tzacatl was probably the most abundant hummingbird on the hacienda. Single birds were observed feeding in 16 well separated areas, all except one of which were centred on *Eugenia* trees. The exception, which was not occupied until near the end of our visit, was centred on a climber, *Psammisia* cf. *penduliflora,* which had just come into flower. Conspecifics, *A. franciae,* and Bananaquits were chased from these territories. Although most feeding records were from *Eugenia, tzacatl* fed on a greater variety of flowers than any other hummingbird, from as low as 0·5 m to tree tops at 15 m. It was only once seen attempting to feed on banana flowers, when it went to a pierce hole probably made by a Bananaquit.

When feeding at *Eugenia, tzacatl* frequently (62% of records) uttered a monosyllabic *chack* between probes, but at small *Eugenias* with few flowers and after 1630 h such calling was rare. At two heaths over which *tzacatl* held feeding territories, *Psammisia* on the hacienda and *Cavendishia* about 6 km away, it also regularly called between feeding probes.

Frequently it gleaned insects from low, thick vegetation, at heights of 0·3 to 3 m (mean 1·9 m), e.g. from moss and the backs of leaves inside thick hedges and bushes, and along the underside of the midribs of banana leaves. It hawked also close to or inside thick vegetation, mainly (27 observations) from perches 4 to 11 m high, less often (6 observations) low over herbaceous vegetation from perches 1–2 m high. Hawking sallies were usually within 1·5 m of the perch and were directed at groups of flying insects, the bird often darting about and catching more than one insect per sally.

Amazilia cyanifrons

Single birds were observed feeding in 12 well separated areas on the hacienda, in nine of which the occupier regularly sang. All were centred on *Eugenia* trees. When taking nectar in these territories *cyanifrons* frequently uttered a monosyllabic *sip,* or *sick,* between probes. Unlike *tzacatl,* it visited *Eugenia* trees standing alone in pastures or along fences, 54% of *Eugenia* feeding records being at such trees. Except for one record at *Hamelia, cyanifrons* was not seen to descend from tree canopy level for nectar foraging. During 2 h watching at several *Cavendishia pubescens* bushes in a tree-shaded ravine 6 km from the hacienda, a *tzacatl* and two *franciae* frequently fed at the *Cavendishia,* but a *cyanifrons* remained in the trees above. Watches at the one flowering *Guzmania* plant, when it had 17 to 19 flowers in bloom, showed a *cyanifrons* silently visiting all flowers at each visit and returning to feed between 15 and 27 min later.

From its *Eugenia* territories *cyanifrons* displaced *franciae* and attempted, often unsuccessfully, to displace Bananaquits. At a territory that overlapped the feeding area of a male *Anthracothorax nigricollis,* the visits of the latter were not disputed. The encounters which presumably established the division of the *Eugenia* trees between *tzacatl* and *cyanifrons* were not witnessed; where the two species had adjoining territories, the occasional silent incursions of one bird into the territory of the other always coincided with the temporary absence of the owner. The choice of *Eugenia* territories by these two *Amazilia* was probably related to their insect-foraging methods, those of *tzacatl* requiring thicker vegetation at canopy, shrub and herbaceous levels while *cyanifrons* foraged for insects in more open places.

Between one and two hours after dawn, boundary encounters occurred between two, three and occasionally four *cyanifrons,* which sang from bare twigs 3–5 m up in an open area and also hawked for insects from the same perches. The insect-hawking recorded during the rest of the day was largely from higher perches (average of 12 records, 8·0 m), nine of them from trees with sparse foliage standing alone in pastures. Hawking sallies were either out from the crown or between the twigs and branches of the crown. There was only one record of *cyanifrons* gleaning for insects.

Amazilia franciae

This was the least abundant *Amazilia* on the hacienda. Only one singing male was located, whose territory, in a coffee and banana patch, a second male attempted to take over. Other males and females were recorded nectar-feeding along the tree-lined river banks and in a second coffee and banana patch. Except for *Eugenia,* the flowers that *franciae* visited had tubular corollas from 15 to 35 mm in length, on average longer than those visited by *tzacatl* (15–19 mm) and *cyanifrons* (15–18 mm). No defence of a feeding territory was observed; all nectar-feeding was silent, in contrast to the territorial *tzacatl* and *cyanifrons,* which frequently called between probes.

Most feeding records were from a male which was trapped and marked with a red dye, and was watched (both before and after being trapped) for a total of 18 h. This bird did much insect-hawking (28% of feeding records). Most sallies were short, about 30–60 cm from the perch, a single insect being captured. Perches used for hawking ranged from 1 to 5 m above ground level (average of 23, 2·5 m), and insects were usually caught close to vegetation, sometimes between the twigs of shrubs or the branches of low trees. Beside insect-catching, this male took nectar from *Canna, Hamelia, Eugenia* and banana flowers within the coffee patch, and also crossed 55 m of rough pasture to visit some *Eugenia* trees which were divided between adjacent territories of a *tzacatl* and a *cyanifrons.* Both of the territory-holders were seen to drive off the *franciae.*

Before 5 August the marked male *franciae* was heard to sing only once in 6 h of observation. Over a 4-day period, 5–8 August, another male *franciae* contested the possession of the territory with the owner. The encounters occurred almost entirely within an area measuring 26 × 14 m and at heights of 2–5 m. During this period, and for some days after the intruder had been ousted, the song output of the marked male was very high, averaging 44 song phrases an hour during the first 3 hours of the day. The intruder also occasionally sang while he was contesting possession. It seemed that the marked male's territorial behaviour was not defence of an insect-foraging area, because a *tzacatl* occasionally hawked for insects unmolested within 2–3 m of where he was perched. Presumably he was defending a potential mating site.

Anthracothorax nigricollis

This species was scarce at the time of our visit. In the first half of the period only a single territorial male was located on the finca; in the second half two more males were present and one or two females.

The first located male was watched for a total of 18 h. It occupied a territory measuring c. 55 × 15 m, containing shade trees 10–13 m tall, old citrus trees, banana plants and a rich herbaceous undergrowth. The territory overlapped the territories of a male *Amazilia franciae* and two *A. cyanifrons.* This bird fed largely by making frequent hawking sallies from exposed perches, often from the highest perch in the territory (13 m) or in the early morning and late evening from lower perches (mean height 10·2 m). In a typical sally it would fly 2–4 m out from the tree and make a number of darts from side to side before returning to its perch. Its territorial activities were almost entirely directed to the protection of the airspace where it hawked. Except for one instance, when it displaced a *Phaethornis guy* from banana flowers, it was not seen contesting nectar sources. All three species of *Amazilia* came to feed at an *Eugenia* about 9 m from its main hawking perch but were not chased off; once it fed at *Eugenia* flowers within 1·5 m of the male *franciae* without any interaction. The male *A. franciae* whose territory overlapped that of the male *nigricollis* also frequently hawked for insects, from perches 1·5 m high, without interference; but on three occasions when it perched about 6 m up on the top of a half-dead citrus tree it was at once chased from the perch by the male *nigricollis*. It was ignored on one of its main perches 4·3 m up in the same tree. On eight occasions the male *nigricollis* chased off conspecific males which perched in his territory or flew over it.

A. nigricollis was seen to visit only two plants for nectar, both introduced (*Eugenia* and banana). Seven intervals between successive visits to the same banana flowers ranged from 19 to 55 min (mean, 37 min). Females were not recorded nectar-feeding, but on two occasions were seen gleaning for insects in thick hedges.

A. nigricollis was one of the nine species of hummingbirds whose feeding habits were studied at tropical levels in Trinidad (Snow & Snow, 1972). Insect-foraging, almost entirely by hawking from high perches, accounted for 38% of the Trinidad records, compared with 45% of all records at Togui. In both places this species fed more on insects than any other resident species of hummingbird.

Chlorostilbon gibsoni

C. gibsoni was the smallest hummingbird species regularly present on the hacienda. All but one of the feeding records were of female-plumaged birds, as were the two birds trapped. It was recorded nectar-feeding low down (0·3–4 m, mean, 1·8 m) in open unshaded pastures and along hedges. It was silent when feeding and did not appear to be territorial.

Of the five plant species visited, *Ipomoea* and *Manettia* were also visited by bees and their concentrated nectar (Table 6) is typical of bee-pollinated flowers. Three morning watches (0605–0805, 0700–0930 and 0935–1035 h) on a hedge where *Manettia* (15–20 flowers blooming) and *Hamelia* (45 flowers blooming) grew side by side, provided evidence that *C. gibsoni* stopped visiting *Manettia* when bees started feeding at it, between 0720 and 0755 h. In all *gibsoni* made 14 visits, returning at intervals ranging from 14 to 34 min (mean, 23 min). On the 8 visits up until 0800 h it visited both plants on 7 occasions and the *Manettia* only on one occasion; on the 6 visits after 0800 h only the *Hamelia* was visited, except at 0816 when the *Hamelia* and one bloom only of the *Manettia* were visited. Bees were not seen to feed at *Hamelia* but very occasionally butterflies did so. Timed feedings showed that *C. gibsoni* was able to exploit *Manettia* flowers more rapidly than *Hamelia* flowers; the time spent probing a flower (about 0·4 s) was almost the same for both plants, but as less time was taken in manoeuvring between *Manettia* flowers the rate of visiting them (one flower per 0·7 s) was higher than the rate for *Hamelia* flowers (one per 1·0 s). During these observations *Amazilia tzacatl* was often in view foraging for insects, and fed at *Hamelia* and at *Ipomoea* growing near by in the same hedge, but made no visit to *Manettia*.

Phaethornis guy

There were extremely few of this species on the hacienda, apparently only one or two females, and the two plants at which they were recorded feeding *(Musa* and *Canna)* were both introduced. A clump of *Heliconia* sp. in a ravine 5 km from Togui was also fed at by *P. guy*. These three herbaceous plants all have long (25–35 mm) curved tubular corollas, matching the bird's long curved bill. The two nests found were on banana leaves and no other plants with suitable leaves were seen on the hacienda. *P. guy* is essentially a forest hummingbird, specialized both in its feeding and in its nest-site (Snow, 1974). Its survival in this intensively farmed area is heavily dependent on the banana, which is planted to provide shade in young coffee plantations, and may be retained or cleared away after the main shade trees have grown.

Discussion

Faegri & Pijl (1966) list a number of morphological features of flowers that characterize the 'syndrome of ornithophily'. Stiles (1979) has extended them to include the phenology, nectar production, spacing on the plant, and other features of floral biology that may impinge on a plant's avian pollinators and thus be subject to coevolutionary selection. On the bird's side, a complex of characters, structural, physiological and behavioural, are related to nectar feeding and are presumed to have evolved in the course of development of the mutual relationship between bird and flower. An extensive and specialized literature has resulted from recent research into nectarivory in birds, with hummingbirds the main subjects. Emphasis has been especially on energetic aspects of the interaction, and the different feeding strategies that have resulted therefrom. It would be inappropriate to attempt here a thorough review of a fast-growing subject, and we confine the discussion to those aspects of the subject on which our observations provide new data or suggest modification of previous opinions.

The syndrome of ornithophily

Faegri & Pijl considered that the toughness that is characteristic of bird flowers is a protective adaptation against damage by the beaks of their avian pollinators, and this opinion seems to have been generally accepted. So far as hummingbird flowers are concerned, however, we think that the protective layers at the base of the flower are generally an adaptation protecting the nectar from nectar thieves and making it available only to legitimate visitors. The hard woody calyx of the pendent flowers of *Huilaea* (p. 119), very different from the rather delicate, insect-pollinated flowers of other melastomes, is a good example. Within the Ericaceae, the flowers of *Cavendishia pubescens* seemed to be effectively protected against nectar thieves by the bracts round the base (p. 120). There seems to be no good evidence that the delicate and exact probing of the bill of a hovering hummingbird damages even soft-tissued flowers.

Protection of a flower's nectar against thieves need not be absolute in order to be effective. At Fonté we had only a single record of the flower-piercer *Diglossa albilatera* piercing the flowers of *Cavendishia cordifolia*, which was very common in places where the flower-piercer was also abundant. The flower of *C. cordifolia* is moderately protected at its base, but is not immune to exploitation by *D. albilatera* (p. 120). It seemed likely that this flower-piercer was generally avoiding *Cavendishia* flowers at Fonté because they could exploit much more efficiently the unprotected flowers of another abundant plant, *Palicourea angustifolia*.

The orientation of the corolla tube is often a good indicator of the degree to which the flower is adapted for hummingbird pollination. This is well illustrated by the three species of *Palicourea* at Carare: in *P.* cf. *vagans*, the least specialized (corolla 9 mm, white; calyx yellow), the corolla tube is horizontal; in *P.* sp. 43 (corolla 15 mm, yellow; calyx red) between horizontal and pendent; and in *P. demissa*, the most specialized (corolla 31 mm, purple), pendent. Similarly *Huilaea* differs from other melastomes in having pendent flowers, and the specialized tree-heaths, e.g. *Psammisia falcata* and *Thibaudia rigidiflora*, from the unspecialized *Disterigma* sp. (Table 4).

The sugar concentration of the nectar, another important aspect of the syndrome of ornithophily, is discussed later in a separate section.

Specialized coevolutionary relationships

Just as a flower may be specialized to a greater or lesser degree for pollination by particular kinds of hummingbirds, so different hummingbird species are specialized to varying degrees for feeding at particular kinds of flower. As the most advanced mutual specialization one might imagine a flower adapted for pollination by only one species of hummingbird, which in turn might be dependent on the nectar of that one kind of flower. In fact it seems that, while very specialized flowers may indeed depend on a single hummingbird pollinator, even the most specialized hummingbirds usually feed from a number of different kinds of flower.

The most striking of the coevolutionary adaptations involving the hummingbirds that we observed is that between *Ensifera* and *Passiflora mixta.* Other species of *Passiflora,* e.g. *P. vitifolia* (Skutch, 1964) and *P. longiracemosa* (Snow, 1973), have flowers with long tubular corollas that are fed at, and probably pollinated, by long-billed hummingbirds, but the present case represents the extreme. It can hardly be doubted that the flowers of *P. mixta* evolved to their present length in step with the bill of *Ensifera.* The range of *P. mixta,* which has its centre of abundance at temperate levels in the Andes of Colombia and Ecuador, corresponds broadly with the range of *Ensifera* (Andes of north-western Venezuela south through Colombia, Ecuador and Peru to northern Bolivia); but *P. mixta* now occurs also in a few scattered localities in the coastal range of northern Venezuela beyond the range of *Ensifera.* This is, however, almost certainly due to introduction by Amerindians, who have long made use of *P. mixta*'s highly edible fruit (S. Tillett, pers. comm.).

We recorded *Ensifera* feeding at no other kind of flower; indeed there were no plants in flower at the time of our visit approaching *Passiflora mixta* in length of corolla. *Ensifera* is, however, generally said to be adapted to feeding at *Datura* flowers. It certainly feeds at *Datura* flowers, but it may be doubted whether this is a case of coevolutionary adaptation. *Datura* flowers have few ornithophilous features; they are widely open at the mouth, so that shorter-billed hummingbirds than *Ensifera* can feed at them by getting their heads well inside the corolla tube (pers. obs.), the anthers and stigma are not exserted so as to come into contact with *Ensifera*'s forehead (as they are in *P. mixta*), and the corolla is thin-walled and easily pierced. We saw no *Datura* growing wild in the area where we worked, but they were common ornamental plants round houses. *Datura* is a small genus of only 10 species, occurring in tropical America but widespread elsewhere in tropical and warm temperature areas. Its pollination has not been thoroughly studied. *D. meteloides* is visited by a hawk moth which enters the corolla tube (Baker, 1961), and the open vase shape of the flowers suggests that they are adapted to facilitate the bodily entry of pollinators rather than to restrict their nectar to pollinators with very long bills or probosces. The white colour of most *Datura* flowers suggests adaptation to a crepuscular pollinator. Two species have red flowers, a colour typical of hummingbird flowers but also found in some moth-pollinated flowers (Baker, *loc. cit.*). We provisionally conclude that *Ensifera* is adapted primarily to *Passiflora mixta* and other species of *Passiflora* with very long corolla tubes, and that its habit of feeding at *Datura* flowers is a result of man's alteration of its habitat. But it would be desirable to study *Ensifera*'s feeding habits in an area, if there be any, where a red-flowered *Datura* grows wild.

Also needing further study is the effect of exploitation of the nectar of *Passiflora mixta* by flower-piercers and the hummingbirds that make use of the holes made by flower-piercers. In the Fonté study area nectar-thieving reduced the amount of nectar available to *Ensifera* to such an extent that it must surely have affected *Ensifera*'s abundance. Yet there is every reason to suppose that these or similar nectar thieves have been present for as long as *Ensifera* and *P. mixta* have existed. Our experimental protection of *Passiflora* flowers showed that *Ensifera* could obtain all the nectar that it could ingest from one or two flowers of the dozen or so available on a plant. Had the experiments continued, it would have been of great interest to have seen whether individual *Ensiferas* would have switched from trap-lining, over what must have been considerable distances, to territoriality at single *Passiflora* clumps. The effect of territoriality, from the plant's point of view, would be greatly to increase the incidence of self-pollination. Trap-lining by *Ensifera,* on the other hand, must promote out-crossing (Linhart, 1973). Hence it might be advantageous for the plant not to evolve increased protection of the nectar from nectar thieves, but to maintain its pollinator at low population densities; but such a course would be hazardous, since it would carry the risk of occasional local disappearance of the pollinator.

Lafresnaya, the only temperate-level Andean hummingbird with a long curved bill, was recorded feeding mainly at three kinds of flowers with long, curved corolla tubes that fitted its bill closely *(Pentadenia strigosa, Castilleja fissifolia, Siphocampylus bogotensis).* None of these flowers was seen to be fed at 'legitimately' by any other hummingbird species. It is reasonable to conclude that *Lafresnaya* is the main pollinator of these three plants, and that their flower structure coevolved with *Lafresnaya*'s bill. The situation is not simple, however: *Lafresnaya* males and females have distinctly different bill-lengths, that of the male being shorter although the male's wing is longer than the female's. This sex difference suggests that the male is likely to be more territorial than the female, and also to be less specialized in its feeding habits (see next section). Our limited observations did in fact suggest that *Lafresnaya* females were trap-liners and that some, at least, of the males held feeding territories.

The only other specialized coadaptations between particular hummingbird species and flowers suggested by our observations were those between the three hummingbirds with long straight bills at Carare, *Coeligena prunellei, C. torquata* and *Doryfera ludoviciae,* and some of the flowers at which they fed. *C. prunellei* and *Doryfera* were the only two hummingbirds seen feeding legitimately on the heath *Psammisia falcata,* whose long corolla tube is filled with densely packed stamens, necessitating a considerable upward thrust by a hovering hummingbird in order to reach the nectar; and *C. torquata* (a smaller species, subordinate to *C. prunellei,* but with an even longer and markedly finer bill) appeared to be the only species capable of exploiting the specialized and very narrow-tubed flowers of *Bomarea* cf. *carderi.*

Trap-lining vs. territoriality

The broad distinction between trap-lining and territoriality as alternative foraging strategies for hummingbirds has been mentioned earlier. Feinsinger & Colwell (1978) have recently made a more refined classification, defining four community roles available to hummingbirds. They distinguish two kinds of trap-liners. 'High-reward' trap-liners are species with either particularly long or curved bills, which have coevolved with certain plant species that offer high nectar rewards per flower, the nectar being inaccessible to other hummingbirds. These are the species usually referred to as trap-liners. 'Low-reward' trap-liners are small, shorter-billed species, which are excluded from clumped flowers by territorialists and instead visit dispersed, unspecialized flowers. Hummingbirds in this second category are not found in all communities. Territorialists form a third category, and the fourth consists of 'territory-parasites', which may either be large birds with moderate-length beaks that can forage with impunity among flowers defended by smaller territorialists, or very small, short-billed species which can infiltrate into territories, often feeding in parts of the territory not much used by the owners. In addition to beak characteristics and body size, wing-disc loading has been shown to be important in fitting a hummingbird for a particular foraging strategy (Feinsinger & Chaplin, 1975). Species with high wing-disc loading (high weight in relation to wing-length) are more manoeuvrable, have greater acceleration, but are less efficient at hovering than species with low wing-disc loading. The former tend to be territorialists (being better in aggressive encounters and having less need for sustained flight), and the latter trap-liners.

The hummingbirds in our study areas fitted into Feinsinger & Colwell's four categories well; but on the basis of available weights and measurements there is no clear relationship between foraging strategies and wing-disc loading. Thus *Ensifera,* the most pronounced trap-liner, has the highest wing-disc loading (·0489) and *Metallura,* a territorialist, the lowest (·0257). *Coeligena torquata,* a typical trap-liner, and *C. prunellei,* a more territorial species, both have wing-disc loadings of ·0281. It is likely that the lack of relationship is due in part to the small samples of weights available to us, some of which are from other areas. We draw attention instead to the ratio between bill-length and wing-length, given as a percentage in Table 1. This proves to be a good indicator of feeding strategy, and has the advantage that it can be consistently derived from museum specimens.

There were 10 species with bill/wing percentages of 38 or over (Table 1), all but two of which were high-reward trap-liners. The two with the highest percentages (*Ensifera* and *Phaethornis guy*) show the highest degree of feeding specialization. The exceptions were *Acestrura mulsant,* which although apparently a trap-liner was not seen to visit any flowers to which it had exclusive or nearly exclusive access. Observations were, however, few. The other exception, *Chlorostilbon poortmani,* was a low-reward trap-liner which exploited the less specialized hummingbird flowers and some bee-pollinated flowers.

Eight of the 12 hummingbirds with bill/wing percentages between 20 and 32 were territorial over high-density, morphologically less specialized ornithophilous flowers (e.g. *Guzmania cryptanta, Palicourea* sp. 43) or over high-density flowers also available to insects (e.g. *Clusia, Eugenia*). They also frequently hawked for insects. Three forest species (*Adelomyia, Ocreatus, Aglaiocercus*), however, were not seen to be territorial. Excluding pierce-hole feeding, 80% of nectar-feeding records for these three species were at flowers also visited by insects, mostly large bees. Some large bees are trap-line feeders at dispersed specialized flowers, and possibly these hummingbirds are adapted in some way to share this nectar source. There were insufficient observations to determine the feeding strategy of *Colibri thalassinus,* but in Costa Rica Wolf *et al.* (1976) found that it defended a specialized hummingbird flower, mostly from conspecifics.

The three *Amazilias* at Togui, the only three congeneric species resident in the same locality, have bill/wing percentages closely related to their observed feeding strategies: *A. franciae,* a trap-liner – 45·2; *A. cyanifrons,* almost entirely territorial over one concentrated nectar source (*Eugenia*) – 32·6; and *A. tzacatl,* territorial over the same nectar source, also over hummingbird flowers with moderate-length corollas, and in addition exploiting a variety of more dispersed plants – 37·1. The two *Coeligena* species at Carare showed slight niche differences which can be related to bill/wing percentages, *prunellei* (38·3) showing some territorial tendencies and *torquata* (40·8) being a trap-liner with possibly exclusive access to one plant species.

Nectar characteristics

The sugar concentration of the nectar of many hummingbird-pollinated flowers is relatively low, averaging about 20% (weight/total weight of solution) (Baker, 1975). Bee-pollinated flowers have more concentrated nectar. The greater dilution of hummingbird nectar is at first sight puzzling, since it has been shown experimentally that, given a choice, hummingbirds prefer the most concentrated solution (Hainsworth & Wolf, 1976). Bolten & Feinsinger (1978) have argued that the dilute nectar typical of hummingbird flowers may have evolved to deter bees, which need more concentrated nectar, and that once a flower has evolved adaptations to exclude bees, selective pressure from feeding hummingbirds may lead to a return to more concentrated nectar. They present evidence from Trinidad in support of this hypothesis.

The flowers whose nectar concentrations are given in Tables 2, 4 and 6 can be divided into three groups: flowers visited by bees as well as hummingbirds (*Aphelandra, Disterigma, Ipomoea, Manettia, Palicourea* cf. *vagans, Phaseolus*); the less specialized hummingbird flowers, with corolla lengths of 11–20 mm (10 species); and the more specialized hummingbird flowers, with corolla lengths of 21–114 mm (9 species). The ranges and means of nectar concentrations for these groups were, respectively, 23–38, mean 29·2%; 14–21, mean 16·8%; and 14–27, mean 19·5%. These figures are in good agreement with Bolten & Feinsinger's hypothesis. It may be noted that two of the morphologically most specialized species, *Passiflora mixta* (25·5%) and *Pentadenia strigosa* (27·0%), had the highest concentrations among the hummingbird flowers.

Ornithophily in the Andean flora

Our data are far too incomplete for any survey of the incidence of ornithophily among Andean plants, and the literature on the subject is very limited; but a few points deserve mention.

It seems clear that three plant families, the Rubiaceae, Ericaceae and Bromeliaceae, are of prime importance, the first mainly for short-billed, unspecialized hummingbirds, the second and third both for unspecialized and for some of the more specialized hummingbirds with long straight bills. In the richest of our three study areas these three families accounted for nearly two-thirds (14 out of 22) of the plant species providing nectar at the time of our visit;

in the two other areas, with poorer vegetation modified by agriculture, the proportions were lower (6 out of 15, and 4 out of 13). Members of the Rubiaceae and Ericaceae provide examples of different degrees of specialization for ornithophily, from such unspecialized flowers as *Palicourea* cf. *vagans* (Rubiaceae) and *Disterigma* spp. (Ericaceae), which have white flowers with short corolla tubes that were visited by insects as well as short-billed hummingbirds, to specialized flowers such as *Palicourea demissa* (Rubiaceae) and *Psammisia falcata* (Ericaceae), which were visited only by two long-billed species. The bromeliads as a family seem to be adapted for pollination by hummingbirds (McWilliams, 1974).

To what extent pollination by hummingbirds has affected speciation and interspecific differences in phenology within these families is a matter for future research. *Palicourea* is a large and taxonomically difficult genus, with about 200 known species (Willis, 1973). Specialization of the flower for pollination by different hummingbird species or groups of species may have led to divergence between taxa (in geographical isolation ?), resulting in reproductive isolation when they later became sympatric. Competition for pollinators between morphologically similar sympatric species may have led to the staggering of flowering seasons, as appears to have happened in Costa Rican *Heliconia* species (Stiles, 1975). It is noteworthy that bromeliads in particular tend to have very restricted flowering seasons, so that observations conducted over a short period give a very incomplete picture of their importance for hummingbirds. The four species that were in flower in our three study areas at the time of our visit were only a fraction of the species present.

The remaining hummingbird flowers belonged to 18 different families (omitting introduced plants), with only one or two species in each. Most of these families are well known to contain ornithophilous genera, the most interesting of the exceptions being the Melastomataceae. This very large family, with numerous neotropical species, is typically insect-pollinated; the flowers are open or have only short corolla tubes. The genus *Huilaea,* with a single species, is known only from a few temperate forest localities in Colombia. Its flowers are strikingly different from typical melastome flowers, showing several ornithophilous features, and it is reasonable to suppose that it evolved in association with forest hummingbirds. Whether it is generally associated with *Boissoneaua flavescens,* which held territories at the *Huilaea* trees at Carare, must await further study.

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A new species of small *Barbus* (Pisces, Cyprinidae) from Tanzania, East Africa.

Roland G. Bailey

Department of Zoology, Chelsea College, University of London, Hortensia Road, London SW10 0QX

A collection of *Barbus* made by the author in northern Tanzania belongs to the group characterized by radiately striated scales and a thin, flexible last unbranched dorsal fin ray. It is described here as a new species.

Barbus venustus sp.nov.

(Fig. 1)

HOLOTYPE. A male fish, 29·0 mm SL from Nyumba ya Mungu reservoir situated at 3°45′S, 37°25′E at an altitude of 670 m on the upper Pangani river, Tanzania, BM (NH) 1979.10.3:1.

PARATYPES. Nineteen fishes from Nyumba ya Mungu reservoir and its affluent streams, BM(NH) 1979.10.3:2–20.

DESCRIPTION. Based on 20 fishes, 19·6–30·2 mm SL.

Body moderately compressed, its depth equal to or, in mature females, a little greater than the length of the head. Predorsal profile convex with a slight nuchal hump. Snout rounded, shorter than the eye diameter which is slightly less than or equal to the interorbital width. Mouth moderate and subterminal. Anterior barbel short, posterior barbel longer, extending as far as the vertical to the mid-point of the pupil of the eye. Well developed sunken pit-lines are present on the cheek and operculum and, less distinctly, on the dorsal surface of the head. There may be as many as 12 lines between the preoperculum and the anterior orbital margin, some branching ventrally. In any line the pits are separated from each other and their mouths may rise above the level of the surrounding skin. Sharply pointed conical tubercles or spinules are developed on the snout and lower jaw of males. The caudal peduncle is relatively slender, its depth 1·36–1·76 (mean 1·56) in its length.

In alizarin stained preparations of two fishes, 26·0 and 27·8 mm SL, the post Weberian vertebral count is 27. The pharyngeal bones and teeth (Fig. 2) are similar in appearance in both specimens. The teeth number 2.3.5–5.3.2 and have recurved crowns.

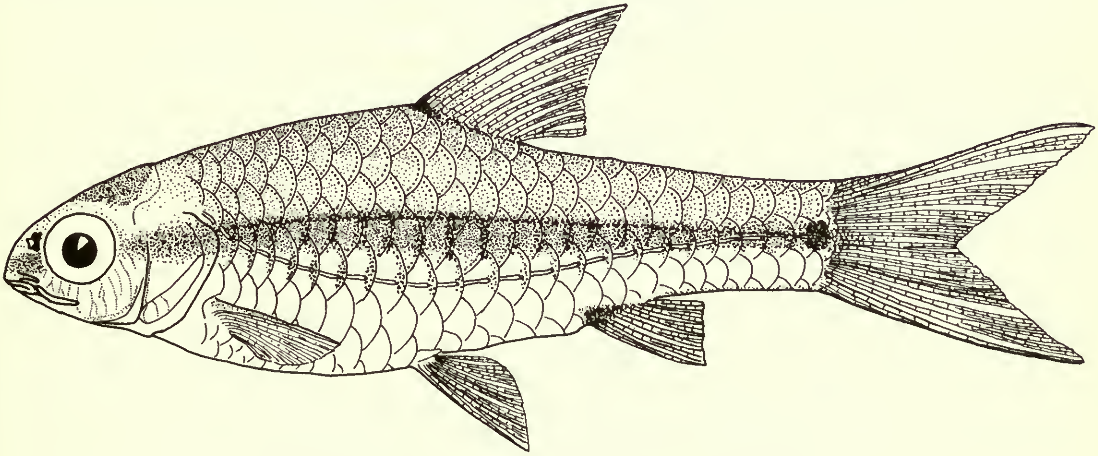

Fig. 1 A paratype of *Barbus venustus*, 27·6 mm SL.

Issued 29 May 1980

Summary of morphometric data for 20 fishes, 19·6–30·2 mm SL; measurements are expressed as percentages of SL.

	range	mean	standard deviation
Maximum depth	28·4–32·4	30·4	1·1
Length of head	27·9–30·4	29·0	0·7
Length of snout	6·3–8·3	7·4	0·6
Horizontal diameter of eye	9·2–11·0	10·2	0·5
Least bony interorbital width	8·3–10·2	9·3	0·5
Length of anterior barbel	0·9–3·0	1·9	0·7
Length of posterior barbel	3·3–5·9	4·3	0·7
Length of longest dorsal fin ray	24·8–28·2	26·9	1·0
Greatest length of pectoral fin	18·8–22·8	20·9	1·1
Distance from snout tip to dorsal fin origin	52·4–56·7	54·2	1·2
Length of caudal peduncle	18·2–21·8	20·1	1·0
Least depth of caudal peduncle	11·9–13·8	12·9	0·6

SCALES. Scales have radiate striae, (Fig. 3). Lateral line complete, with 22 (f.1), 23 (f.7), 24 (f.6) or 25 (f.6) pore-bearing scales; its course dips ventrally on the flanks and returns to a midlateral position on the caudal peduncle. There are 4½ (f.14) or 5 (f.6) scales between the dorsal fin origin and the lateral line and 1½ (f.4) or 2 (f.16) scales between the lateral line and pelvic insertion. Eight (f.3), 9 (f.11) or 10 (f.6) scales encircle the least circumference of the caudal peduncle and 9 (f.15) or 10 (f.5) are found in the pre-dorsal fin row.

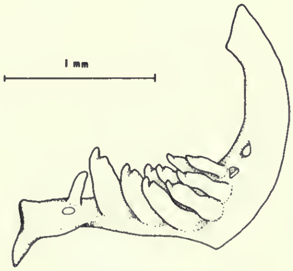

Fig. 2 A lateral view of the right pharyngeal bone from a fish 27·8 mm SL.

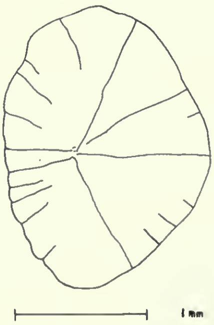

Fig. 3 Striations on a flank scale from above the lateral line.

FINS. The origin of the dorsal fin is on or slightly in advance of the perpendicular to the pelvic fin insertion. It has III/7 (f.7) or III/8 (f.13) rays, and the third unbranched ray is unossified and flexible. The anal fin has III/5 rays. In both fins the last branched ray is typically divided to its base. The pectoral fin does not reach the base of the pelvic fin.

COLORATION. In the preserved fishes, fixed in formalin, the dorsal surface of the head and body are brownish. Scales on the upper flanks and caudal peduncle are outlined in a reticulum of tiny spots and those of the lateral line series are intensely pigmented above and below the pores. A dark midlateral stripe of varying intensity runs from the tip of the snout to the base of the caudal fin. There is a small, rounded black spot at the base of the caudal fin and patches of pigment about the origin of the dorsal and, more distinctly, on the base of the anal fin.

In life, the upper flanks, caudal peduncle and caudal fin are orange-red in colour.

ETYMOLOGY. The specific name is derived from the latin for pretty, and alludes to the attractive appearance of this small fish in life.

DIAGNOSIS AND AFFINITIES. *Barbus venustus* belongs to the group of African *Barbus* characterized by radiately striated scales and a thin and flexible last unbranched dorsal fin ray. It is separable from 12 other species in this group recorded in East Africa by its possession of a combination of the following features:-

small adult size (20–30 mm SL),
well developed pit-lines on the head,
two pairs of short barbels,
relatively large scales (22–25 in the lateral line, 8–10 around the caudal peduncle),
a complete series of lateral line pore scales, and
a dark midlateral stripe extending from the snout tip to the base of the caudal fin where it terminates in a prominent spot.

Cephalic pit-lines have been reported in three other species present in East Africa. Two of these, *Barbus radiatus* Peters (a widely distributed polytypic species, Stewart 1977) and *B. profundus* Greenwood (Lake Victoria), are placed in the subgenus *Enteromius* (formerly *Beirabarbus,* see Greenwood 1970) on the basis of the form and arrangement of the pits. In this subgenus they are small, numerous and tightly packed in raised lines or ridges, (Greenwood, 1962). The pit-lines in *B. venustus* are well developed but from a comparison with those in *B. radiatus* from Tanzanian localities, they clearly differ from the *Enteromius* type being sunken, with rows of relatively large, discrete pits. This condition conforms more closely to that in *B. cercops* Whitehead (Lake Victoria basin), except that only 5 or 6 lines are visible on the cheek in this species compared with up to 12 in *B. venustus. Barbus cercops* also differs from the new species in coloration and the possession of two pairs of long barbels (equal to or longer than the eye) and smaller scales (29–32 in the lateral line series; 12 around the caudal peduncle).

Whitehead (1960) considered that the nearest relatives of *B. cercops* were to be found in western Africa and Greenwood (1962) suggests the possibility of a phyletic significance in the fact that, of 14 species of small *Barbus* he examined with pit-lines of the non-*Enteromius* type, all except *B. cercops* were essentially West African in distribution. Subsequently Hopson A. J. & J. (1965) added a further 11 species with weakly developed pit-lines to Greenwood's list: all are from the Volta region. However, Poll & Lambert (1961), Poll & Gosse (1963) and Poll (1976) have found small *Barbus* with pit-lines of this sort in localities in the north-east, central and south-eastern parts of the Zaire basin. Moreover Tweddle collecting in Malawi (personal communication) has noted pit-lines in several as yet unidentified *Barbus* species and I have observed 5 or 6 weak pit-lines on the cheek in type material of *B. barnardi* Jubb, (AM.P1055, 1056–1062) from the Zambezi river system. It is possible therefore that pit-lines have been overlooked in small *Barbus* from other parts of Africa. As Greenwood (1962) comments, preservation undoubtedly affects the ease with which pits and pit-lines may be seen.

Within the group defined above, the affinities of *B. venustus* are unknown. Although clearly separable in body shape, the depth of the lateral line scales and coloration, the distribution of the pit-lines in *B. schoutedeni* Poll & Lambert (River Dungu, Zaire) appears to be very close to their condition in *B. venustus. Barbus pygmaeus* Poll & Gosse (Central Zaire basin) shares with *B. venustus* a small adult size (<20 mm SL), large scales and a midlateral stripe, but there are only 4 pit-lines beneath the eye and it has a deeper body, longer barbels (about equal to or longer than the eye) and higher dorsal and anal fin ray counts (III/9 and III/6, respectively).

DISTRIBUTION. *Barbus venustus* is known only from the type localities.

BIOLOGY. *Barbus venustus* in the reservoir, was caught in shallow water among open stands of the emergent grass *Paspalidium geminatum.* The sample was obtained in July and August at the onset of the dry season but with the lake level still close to its maximum.

Cladocerans, insect fragments (including mayfly nymphs and chironomid midge larvae), plant material and fine sand were recorded in the guts of dissected fish. Most specimens of both sexes in the sample were sexually mature. The number of eggs, <0·8 mm diameter, carried by two ripe females, (27·6 and 30·2 mm SL) were 190 and 170, respectively.

Acknowledgement

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A new species of *Barbus* (Pisces, Cyprinidae) from Africa

K. E. Banister
Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Barbus amboseli sp. nov.

TYPICAL SERIES. Holotype (BMNH 1979.9.4:1), 35·5 mm SL; paratypes 23–45 mm SL BMNH 1979.9.4:2–6. All these specimens were caught in the Amboseli National Park, Kenya by R. Horowitz.

ETYMOLOGY. The specific name refers to the National Park, their only known locality, and is to be treated as a noun in apposition.

DESCRIPTION. The description is based on the six known specimens listed above. The abbreviations in the table below are explained at the end of the paper. Unless stated otherwise all measurements are expressed as a percentage of the standard length.

Table 1

SL (mm)	35·5	45	35	33	25	23
D	29·6	27·8	30·0	31·8	30·0	26·1
H	28·2	28·9	28·6	28·8	30·0	30·4
I	7·0	6·7	5·7	6·0	6·0	6·5
IO	9·8	10·0	10·0	10·6	10·0	10·8
MW	5·6	5·5	4·9	6·0	6·0	5·4
Pct	19·7	21·1	21·4	18·2	18·0	?
Cpl	19·7	25·6	21·4	22·7	24·0	21·7
Cpd	11·2	12·2	11·4	12·1	10·0	10·9
Snt	8·4	6·7	8·6	9·1	8·0	8·7
Ab	+	6·7	+	?	–	–
Pb	5·6	7·8	7·2	6·6	6·0	5·4
Dsp	15·5	14·5	15·7	13·6	18·0	17·4
Dfin	III–7	III–7	III–7	III–7	III–7	III–7
Pfin	I–15	I–15	I–15	I–15	?	?
Vfin	I–7	I–7	I–7	I–7	?	?
Afin	III–5	III–5	III–5	III–5	III–5	III–5
Cpsc	10	10	10	10	8	10
Ll	20	19	20	20	20	20
Tvl	4½–4½	4½–4½	4½–4½	4½–4½	?	?

The overall shape of this stocky species can be seen in Fig. 1. The great majority of the meristic and morphometric characteristics do not differ significantly from those found in many other species of small *Barbus*. There are, however, two interesting exceptions to this conformity. Firstly, the lateral line scale count is unusually low (see above) and only the largest specimen has lateral line tubules; tubules are completely lacking in the others. Secondly, the anterior barbels appear to develop late. They are present in the largest specimen, incipient in the specimens of 35 and 35·5 mm SL but lacking in the three smallest specimens (Figs 2–4). A pharyngeal bone is shown in Fig. 5, the pharyngeal teeth number 5.3.1 (f.4) or 5.3.2. (f.1). There are 30 (f.2), 31 (f.3) or 32 (f.1) vertebrae excluding those comprising the Weberian mechanism but including PU_1+U_1. In all the specimens there are

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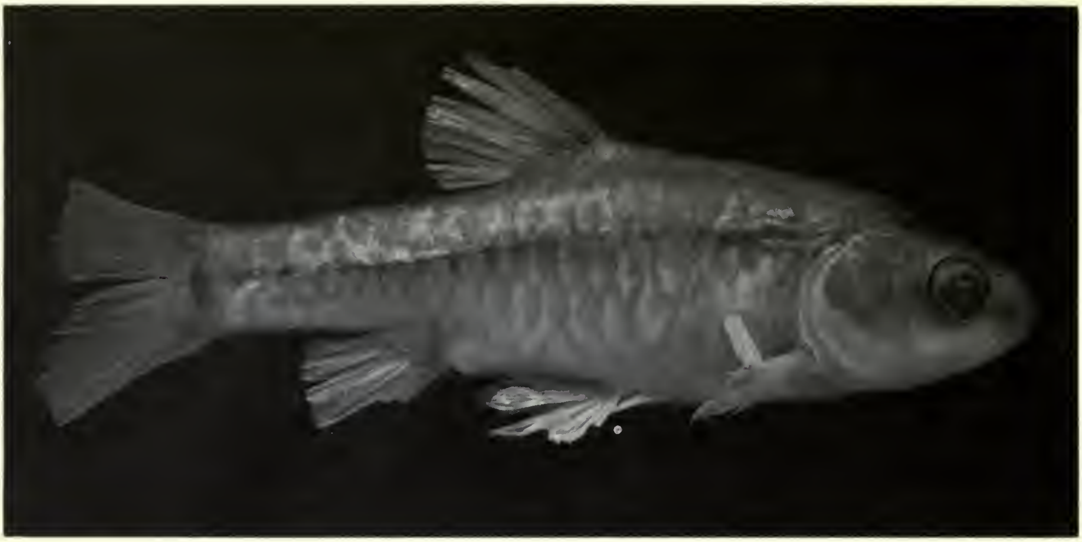

Fig. 1 *Barbus amboseli* Holotype

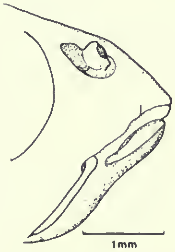

Fig. 2 Head of the specimen of 23 mm SL. Note the absence of the anterior barbels.

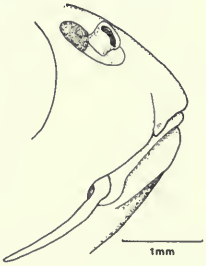

Fig. 3 Head of the fish of 35 mm SL. Note incipient anterior barbels.

three unbranched dorsal fin rays, the posterior of which is strengthened and serrated on its posterior face. There are 3 (f.3) short, hooked gill rakers. The scales have widely-spaced radiating striae (Fig. 6).

The coloration in life is unknown, apart from a verbal comment by the collector that it was 'unremarkable'. Formalin-fixed and alcohol-preserved specimens are brown ventrally and darker brown dorsally. Immediately behind the operculum there is a diffuse dark spot which, after three scales, forms a very narrow clearly defined mid-lateral stripe. One dark spot surrounds the insertion of the unbranched dorsal fin rays, another dark spot is present at the termination of the mid-lateral stripe. There is a slight concentration of pigment cells

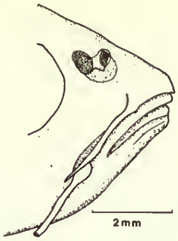

Fig. 4 Head of the largest fish, 45 mm SL. The anterior barbels are well developed.

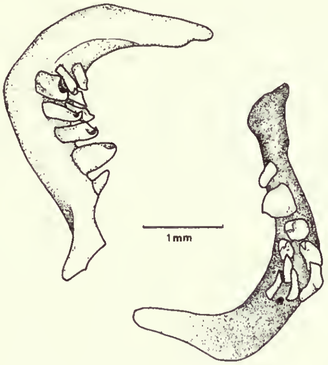

Fig. 5 Two views of the left pharyngeal bone of the largest fish.

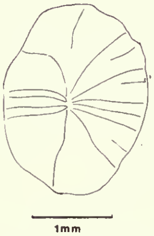

Fig. 6 The third scale from the 'lateral line series' of the holotype to show the striations.

around the insertion of the unbranched anal fin rays. The edges of the flank scales are darker than the centres.

The dorsal fin, anal fin and caudal peduncle spots are more clearly demarcated in the smaller specimens. In the largest specimens, the proximal parts of the dorsal fin rays are more pigmented, especially those of the last simple ray.

Distribution. This species is known only from the type locality, the east side of the Encongo swamp, south of the causeway, Amboseli National Park, Kenya. The waterway was described by the collector as a stream with alternating riffles and papyrus-lined pools, 2–5 feet wide and 1–3 feet deep. The Amboseli area is a region of internal drainage, the lowest part, in wet years, forming the shallow, saline Lake Amboseli.

Diagnosis and affinities. The combination of a serrated dorsal spine, low lateral line count, complete absence or full complement of tubules on the lateral line scales, a 5.3.1. pharyngeal tooth pattern and the late development of the anterior barbels is unique among the small *Barbus* of east and central Africa.

Throughout Africa, very few species have as few scales as *Barbus amboseli. Barbus jae* from Cameroons has 20–23 scales in the lateral line series (*fide* Boulenger, 1911); *B. pumilis*

Blgr from the White Nile has 19–21 (*fide* Boulenger, 1911); *B. chiumbeensis* Pellegrin from Angola has 17–22 (*fide* Poll, 1967). Although *Barbus gribinguensis* Pellegrin was described as possessing 18–22 scales (see e.g. Poll & Lambert, 1961) it has now been shown that Pellegrin erred in his counts (Blache, 1964:120). *Barbus gribinguensis* is now considered to be conspecific with *Barbus pleuropholis* and has 21–23 scales in the lateral line series.

The complete absence of lateral line tubules in all the sample except the largest *Barbus amboseli* is a puzzling phenomenon that immediately invites two possibilities. Firstly, their development could be delayed. Should this be the valid explanation then it would be a most unusual event. Lateral line tubules normally develop along with scales formation in African *Barbus* species (personal observations.). For example, in *Barbus neumayeri* from east Africa scales become distinguishable between 10 and 20 mm SL. Tubules are detectable in the better formed lateral line scales at less than 20 mm SL and the full complement of tubules is conspicuous at 22 mm SL (personal observations.).

Another possibility is that *Barbus amboseli* is unusually variable in the degree of tubule development. Various other species of small *Barbus* from Africa have only a few lateral line tubules, the exact number of which varies. Of the species with a low lateral line count listed above, *Barbus jae* for example, most frequently has only two or three tubules but it is not rare to find specimens in which they are wanting. In *Barbus pumilis* only the first few scales of the lateral line are perforated. Although reduction in the number of lateral line tubules is a derived character, its presence in the species listed above does not imply that they form a monophyletic group. Rather, it seems that the character has been acquired independantly. *Barbus pumilis,* for example, has been considered by some authors (e.g. Poll & Lambert 1961) to belong to the sub-genus *Clypeobarbus* because of its conspicuously deep lateral line scales and its smooth, flexible dorsal fin 'spine'. Also, neither *Barbus pumilis* nor *Barbus jae* have barbels. Amongst others, a similar reduction in lateral line tubules occurs in the strikingly marked, large scaled and sexually dimorphic *Barbus papilio* and its relatives from Zaire (Banister & Bailey, 1979). Again, this group of species is not advocated as close relatives of *Barbus amboseli.* The only obvious common factor in all the species showing reduction in the lateral line tubules is that they are small species, and all have a low number of lateral line scales. However, the correlation is far from perfect because the dull, but sexually dimorphic, species *Barbus haasianus* from southern Africa has 35–38 'lateral line' scales yet lacks the tubules (Jubb, 1967); whereas *Barbus chiumbeensis* has all 17–22 lateral line scales perforated (Poll, 1967).

A serrated dorsal fin spine occurs in approximately a third of the African *Barbus* species. It is impossible, at the moment, to know whether or not the type of dorsal fin spine can be used as an indicator of relationship. Most African *Barbus* species can be divided into three groups on the basis of their type of dorsal fin spine (Boulenger, 1911). The spines can be ossified and smooth, ossified and serrated or unossified, smooth and flexible. The difficulties inherent in the use of these characters to establish phylogenetic relationships are a) our inability to determine which (if any) of the three states is derived (or, indeed, primitive), b) the fact that some apparently valid species have more than one state [e.g. *Barbus miolepis fide* Poll & Lambert 1964 and *Barbus issenensis fide* Almaca 1970 (now regarded as *Barbus capito* by Karaman 1971)] and c) the apparent incompatability of classification by spine type with classification by size i.e. into the 'big' and 'small' *Barbus* species, or by the type of scale striations (parallel or radiate).

Which, if any, of these three commonly used schemes will result in a phylogenetic classification is unknown and great caution should be exercised in adopting one scheme in preference to another.

The commonest configuration of pharyngeal teeth among African *Barbus* is 5.3.2 (inner to outer rows). Reduction from the 5.3.2 pattern (which, on the principle of commonality is the plesiomorph condition) is known in a few species; mostly the 'smaller' ones (Banister, 1973 and personal observation.). The commonest form of reduction in the smaller species is to lose the first tooth of the inner row resulting in a 4.3.2. pattern (Banister & Bailey, 1979 and personal observation.). As far as I know the 5.3.1 pattern present in most of the *Barbus* *amboseli* specimens is unique among the 'small' *Barbus* of Africa, although it reflects the general trend towards reduction in pharyngeal tooth number in the smallest species. The actual loss of the tooth is probably a physical response to the increasing diminution in size.

The late development of the anterior barbel presents an intriguing problem. The number of barbels has achieved a great significance in the classification of *Barbus* species, some authors having given separate generic status to species with respectively 0, 2 or 4 barbels (e.g. Schultz, 1957). Increasing awareness of the considerable variability shown by many species has, therefore, inevitably caused doubts about the usefulness of barbels as characters above the species level. Even at the specific level, great care must be exercised in using barbel characteristics as diagnostic features. *Barbus anoplus* Weber, from South Africa, has populations with only the posterior pair of barbels, populations with four barbels and populations in which the females have only the posterior pair whilst the males develop the anterior pair as well (Jubb, 1967). In an apparently closely related species, *B. motebensis* Steindachner the anterior pair of barbels may or may not be present. Parenthetically, it should be noted that in both these species the number of lateral line tubules is also very variable (Jubb, 1967), although it is not known if this phenomenon can be linked with barbel development *Barbus brevipinnis* Jubb has populations with 2 or 4 barbels. *Barbus brevipinnis,* and to a lesser extent *Barbus motebensis,* have restricted ranges and Jubb (1967:91) has noted that there is often more variability in localised species. In contrast, however, *Barbus anoplus* is widespread.

There was no particular significance in the selection of these examples, they were chosen at random from the literature to illustrate barbel variability. *Barbus amboseli* has an apparently limited distribution which, following Jubb's (1967) comment, might indicate that a great variability is likely. But the only possible significantly variable feature in the regrettably small sample is in barbel number. It has proved impossible to determine the sex of the specimens so the presence of the anterior barbels cannot be shown to be a sex-limited feature as in some populations of *B. anoplus.* Perhaps more usefully, though, a clinal explanation can be rejected because all the specimens came from the same site. Unless a larger sample becomes available I cannot elaborate on the statement that *Barbus amboseli* is unique in that the development of the anterior pair of barbels is a correlate of size and hence age.

The relationships of *Barbus amboseli* are presently unknowable because, within a cladistic framework, its diagnostic features are of no significance.

Acknowledgements

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Key to the abbreviations

Ab	Length of the anterior barbel
A fin	Number of rays in the anal fin
BMNH	Register number in the British Museum (Natural History)
Cpd	Least depth of the caudal peduncle
Cpl	Length of the caudal peduncle
Cpsc	Number of scales around the least circumference of the caudal peduncle
D	Greatest depth of the body
D fin	Number of rays in the dorsal fin
Dsp	Length of the last unbranched ray of the dorsal fin
H	Head length from the tip of the snout to the extremity of the opercular bone
I	Horizontal diameter of the eye
Ll	Number of scales in the lateral line series (or the equivalent series in the specimens lacking the tubules)
MW	Greatest width of the mouth
Pb	Length of the posterior barbel
Pct	Greatest length of the pectoral fin
P fin	Number of rays in the pectoral fin
SL	Standard Length
Snt	Length of the snout from its tip to the anterior border of the orbit
Tvl	Number of scales in transverse series from the origin of the dorsal fin to the lateral line and thence to the mid-ventral line
+	Character present but not measurable
–	Character absent
?	Uncountable or unmeasurable because of size or damage

All measurements were taken with dial calipers.

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A new blind cyprinid fish from Iraq

K. E. Banister

Zoology Department, British Museum (Natural History), Cromwell Road, London SW7 5BD

M. K. Bunni

Natural History Research Centre, University of Baghdad, Bab-al-Muadham, Baghdad, Iraq

Introduction

Trewavas (1955) described a cavernicolous cyprinid, *Typhlogarra widdowsoni*, from a sink-hole near Haditha, Iraq (±34°4′N, 42°24′E). Earlier, A. G. Widdowson had captured examples of *Typhlogarra* from a deeper sink-hole called the Pidgeon Hole (*sic*) (Widdowson 1954) but none of these reached England. On October 21, 1977, Basim M. Al-Azzawi, a fish collector in the Natural History Research Centre, University of Baghdad, visited a sink-hole at the Sheik Hadid shrine near Haditha to collect some specimens of *Typhlogarra*. The significance of this visit is that it revealed two species of cavernicolous cyprinids, *Typhlogarra* and the new species which we have pleasure in naming after Basim Al-Azzawi.

Recently, Greenwood (1976) described a blind, depigmented loach, *Noemacheilus smithi*, which shares its subterranean waters in the Zagros mountains with *Iranocypris typhlops*. Here was the first Asiatic cave system known to support two fully cave-adapted species. The rarity of this event was emphasized by Greenwood (1976) who thought that the Zagros mountain situation was paralleled only by that in the Mammoth Cave, Kentucky. To that very short list we can add only the poorly known Yardee Creek Wells, Northwest Australia where the synbranchid *Anommatophasma candidum* Mees (= *Ophisternon candidum fide* Rosen & Greenwood 1976) and the goby *Milyeringia veritas* Whitley occur (Mees 1962), and now the waters below Haditha.

Caecocypris basimi gen. et sp. nov.

COMMENTS ON THE GENERIC STATUS OF THE TAXON. Until recently, it was accepted practice to consider a cavernicolous species as generically distinct from its nearest epigean relative. The absence of e.g. eyes and pigment were implicitly regarded to be of more 'taxonomic' importance in determining the rank of the taxon than any similarities that the hypogean species and its relatives may possess. The characin *Anoptichthys jordani* Hubbs & Innes, the cyprinid *Caecobarbus geertsi* Boulenger and the synbranchid *Typhlosynbranchus boueti* Pellegrin demonstrate, by their allocated generic names, the theory behind this approach. Recent reconsiderations of some cavernicolous species on a phylogenetic basis have shown the illogicality of a generic level separation for the hypogean member of an epigean genus. Indeed, Greenwood (1976) wrote in his description of the cavernicolous *Noemacheilus smithi* 'Certainly no useful or phyletic purpose would be served by creating for it (*N. smithi*) a new genus that could only be defined on the basis of such features as eyelessness, depigmentation and other regressional trends associated with cave life....' *Typhlosynbranchus boueti*, mentioned above, has now, on phyletic grounds, been transferred to the epigean genus *Monopterus* by Rosen & Greenwood (1976). *Anoptichthys jordani* and its subterranean congeners, which have been the subjects of many biological studies, have been shown to be interfertile with the epigean *Astyanax mexicanus* and have frequently been called as such although (as far as we are aware) the genus '*Anoptichthys*' has not been formally synonymised with *Astyanax* (see details and bibliography in Mitchell, Russell & Elliott 1977). Roberts and Stewart (1976:304) could find no reason for maintaining a separate genus for the blind, rheophilic spiny eel *Caecomastacembelus brichardi*;

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consequently, they placed *Caecomastacembelus* in the synonymy with *Mastacembelus*. Although the phyletic reasonableness of these nomenclatural changes cannot be denied, they are only practicable when the closest epigean relative of the hypogean species has been detected.

The reason behind our decision to place our new species in its own genus is that we have been unable to discover its relationships below the family level.

Holotype. The holotype is a mature female, 49 mm SL, BMNH 1979.8.3:1 from a natural well in the Sheik Hadid sink hole, Haditha, Iraq. A further eight specimens 7·9 mm–36 mm SL from the same locality, BMNH 1979.8.3:2–9 are paratypes.

Description. The description is based on nine specimens, 7·9–49 mm SL.

SL	49 mm	36 mm	31 mm	30·5 mm	30 mm	27 mm	24 mm	22 mm	7·9 mm
D	21·4	20·8	16·4	16·4	15·0	?	?	?	11·4
HW	18·3	19·4	19·0	19·8	18·4	20·4	?	?	16·5
HL	30·6	30·6	32·2	30·8	30·0	29·7	?	?	26·2
MW	10·6	11·1	9·8	11·5	8·5	11·1	?	?	7·8
Cpl	13·9	14·0	14·8	15·6	15·0	15·5	?	?	–
S-D	54·0	55·5	51·5	54·0	55·0	53·6	?	?	46·5
Ll	29	28	28	29	31	?	29	30	–
Cpsc	12	12	12	?	12	?	?	?	–
D fin	III 7	III 9	III 7	III 8	III 8	III 8	III 8	III 8	7
C fin	I-9-9-I	I-9-8-I	?	I-10-8-I	?	I-9-8-I	I-9-9-I	?	19
A fin	II 5	II 5	II 5	II 5	II 5	II 5	II 5	II 5	4
V fin	II 6	II 7	I 8	II 7	II 7	II 7	?	II 7	–
P fin	II 13	II 13	I 15	?	I 13	II 14	?	II 13	–
Gr	14	12	13	14	13	?	?	?	?

Unless stated otherwise all measurements are expressed as a percentage of the standard length. The key to the symbols will be found on p. 158.

The body is nearly circular in cross section in the abdominal region but becomes progressively compressed caudad. The head is slightly depressed. The mouth is horse-shoe shaped in ventral view. The gape is oblique (Fig. 1) and it extends as far as the vertical from the middle of the nostrils. The lips are thin and covered with minute, hair-like villi. There are no barbels. At their symphysis, the dentaries are produced into a small knob, but there is no corresponding notch in the upper jaw. The gular region has a padded appearance and lacks the mental disc characteristic of the sympatric *Typhlogarra widdowsoni*.

On the cheek there are five or six approximately vertical rows of inconspicuous pits which resemble the 'pit organs' found in some other cyprinids. The smallest specimen has a number of protuberant structures randomly distributed over the lower parts of the sides of the head. The relationship, if any, between these and the 'pit organs' on the larger specimens is uncertain.

Excluding the smallest fish (see below), and that of 24 mm SL, all the specimens have a small slit marking the position of the eye. The orbit is filled by fat globules bound together with loose connective tissue. The 24 mm specimen lacks the slit. In the only specimen (36 mm SL) in which the orbital region was dissected there was no trace of the eye in the left orbit, but in the right orbit there was a small structure (Fig. 2) which we interpret as a very regressed eye. This consists of a small tough sphere with two strap-like bands running rostrad towards the anterior wall of the orbit. From the posterior part of the sphere there are two thin, thread-like bands which appear to have fastened onto the inter-orbital septum. The two sets of bands are tentatively interpreted as residual eye muscles. Histological examination will be necessary before we can have any confidence in our identification of these structures.

The smallest fish has a vestigial eye visible through the translucent tissue (Fig. 3). There is

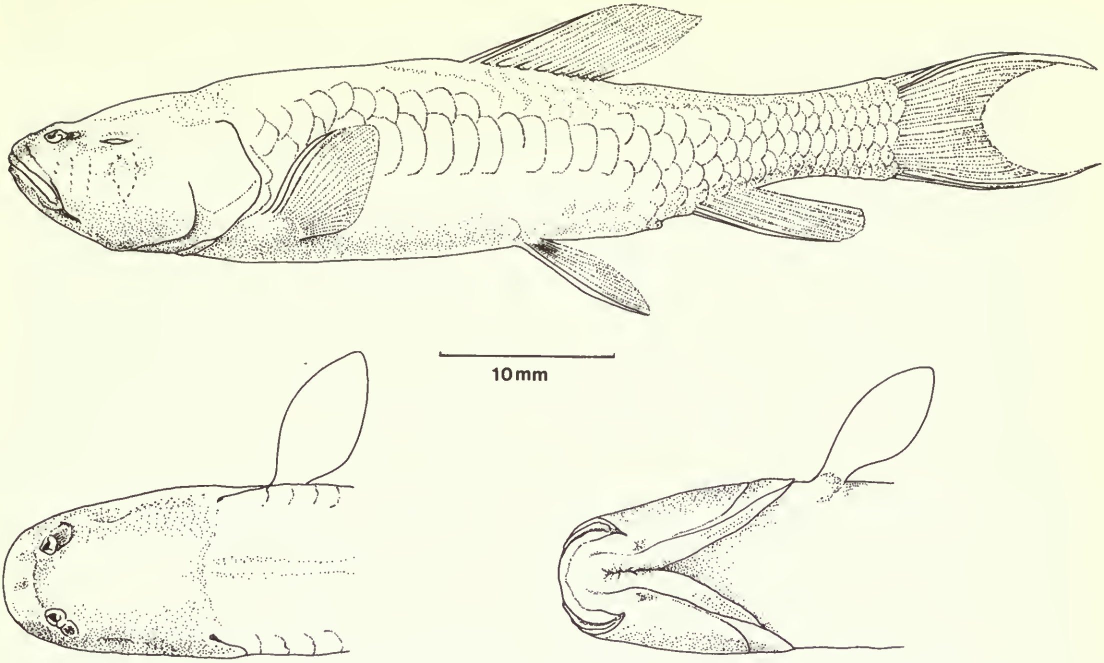

Fig. 1 *Caecocypris basimi* Lateral view (above), dorsal and ventral views of the head (below)

a small spherical lens and faint traces of pigment manifest as pale brown stains forming a ring around, particularly, the dorsal and posterior parts of the lens.

The cephalic lateral line canals are not enlarged. The nostrils are situated at the lateral margin of the flat top of the head almost at the level of the supraorbital bone. The margin of the anterior nostril is produced into a short tube, that of the posterior is flush with the surface of the head. In the specimen of 36 mm SL there are four thick sensory folds on each side of the central nasal lamella.

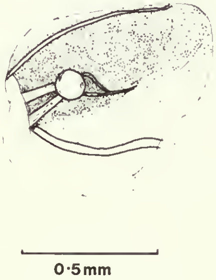

Fig. 2 Right orbit of the specimen of 36 mm SL.

The isthmus is relatively short and broad, and is not joined to the branchiostegal membrane. This condition is rare in cyprinids and, to the best of our knowledge, does not occur in any other cyprinid in the Tigris and Euphrates system.

The gill rakers are short and slightly curved. The number on the lower limb of the first gill arch is given on p. 152. The position of the fins can be seen in Fig. 1 and the number of rays is given on p. 152. All the simple rays are thin, flexible and smooth. The fins of the smallest example are in the process of differentiating. The pectoral fin is rayless and is carried on a pedicel as is usual in the larval condition. The dorsal fin rays are formed and the fin is separate from the median fin fold. The anal fin is still linked to the median fold and the rays are just beginning to develop.

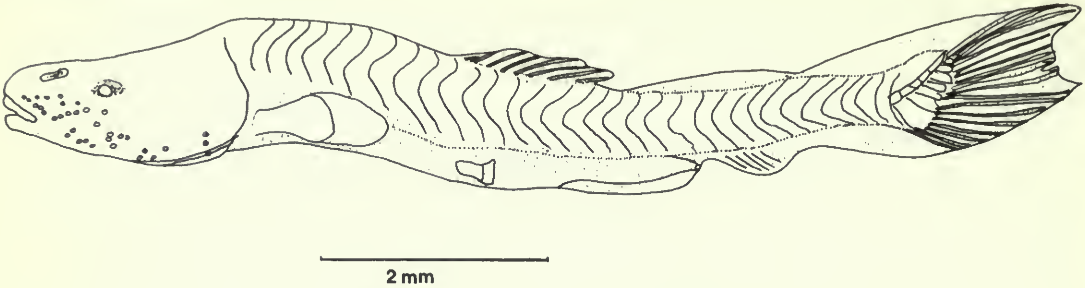

Fig. 3 *Caecocypris basimi* 7·9 mm SL.

In the five specimens radiographed there are 32 vertebrae excluding those comprising the Weberian mechanism and including PU_1+U_1. It is difficult to identify positively the first caudal vertebra from radiographs but there seems to be sixteen or seventeen abdominal vertebrae. Ten pairs of ribs are present. Dorsal and ventral intermuscular bones are poorly ossified and can only be detected posterior to the dorsal fin. The caudal fin skeleton does not appear to differ from the general cyprinid type. The alimentary canal is relatively short with only one major coil and is less than twice the body length. The holotype (a mature female) has over thirty large eggs visible as well as many more less mature ova. The largest eggs are over a millimetre in diameter.

The pharyngeal bones are delicate and bear two rows of slender, conical teeth arranged 5.1–1.5 (f.3). The posterior edentulous process forms a right angle with the rest of the bone.

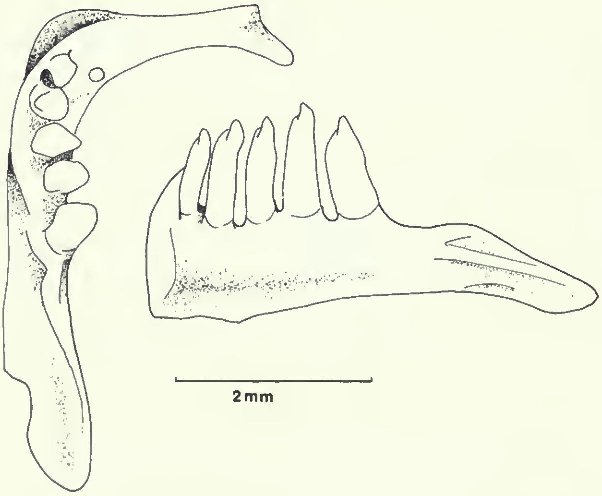

Fig. 4 Left pharyngeal bone of the holotype of *Caecocypris basimi.* Occlusal and ventral aspects.

SQUAMATION. Scales are present only on the larger specimens. A mid-lateral row (corresponding to the lateral line series in other cyprinids, but in this case distinguished by the absence of lateral line tubules) of scales are the best developed, but even they are thin and flexible. Several scales tore during their removal. The biggest fish has a complete mid-lateral row as well as scales over the whole of the caudal peduncle. The back, in front of the dorsal fin, and the abdominal region are scaleless. Above and below the mid-lateral series, in front of the caudal peduncle, there are a few poorly-formed scales. The scales of the mid-lateral series and, to a lesser extent, those on the sides of the caudal peduncle are unusual in that they are deeper than long. The scale striations are more or less parallel (Fig. 5). Scale counts are given on p. 152.

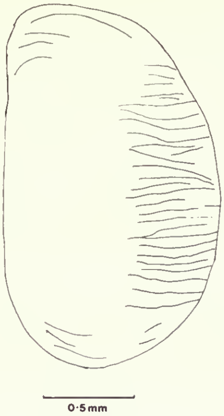

Fig. 5 Scale from the holotype to show the striations.

COLORATION. In life the fish was dead-white suffused with pale pink. The branchial region was deep red, the colour of the blood showing through the translucent tissues. The fins were colourless and there did not appear to be any guanine on the body. Specimens fixed in formalin then preserved in alcohol are an opaque, flat white colour with translucent, pallid fins.

THE LOCALITY. The specimens were collected in a sink-hole near the top of a small hill surmounted by the Sheik Hadid shrine. The hill is some 500 m to the west of the Euphrates on the northern outskirts of the town of Haditha. A few metres to the west of the shrine is a small quarry formerly a source of limestone for building. Access to the sink-hole is via an opening, 2–3 by 6 m, on the floor of the quarry. Below this opening is a cavern, 6 by 6·5 m, its stone-covered floor some 5 m below the quarry floor. At the eastern end of this cavern i.e. the side next to the hill, is natural well with surface dimensions of 1–2 m by 3–4 m and a depth of about 2 m. The water enters the well from four sources, two narrow slits and two oval apertures, about 15–30 cms deep. At the time of collection the greatest depth of water

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Details of the water analysis from the Sheik Hadid well
Provided by the Department of Chemistry and Minerals, Iraq Foundation General of Minerals

Date 16.6.1979
pH 7·5
Non-Carbonate hardness 23·85 mgl^{-1}
Total dissolved solids @ 22° C 3072 mgl^{-1}

Cations	mgl^{-1}	*Anions*	mgl^{-1}
Na^+	490	Cl^-	912·84
K^+	44·8	SO_4^{--}	1020·64
Ca^{++}	265·53	NO_3^-	nil
Mg^{++}	182·4	NO_2^-	nil
		CO_3^{--}	18·0
		HCO_3^{--}	231·84

was 63 cms, but in spring the water table rises to fill the well. The well is shaded from direct sunlight by a rock shelf at the eastern edge of the sink-hole opening; only in late afternoon would direct sunlight reach the well.

In all probability, the type locality of *Typhlogarra* (the Haditha hole of Trewavas, 1955) is the sink hole described above. There are no other sink-holes in the area that match the description given by Trewavas (1955). Widdowson's Pidgeon hole is a much deeper sink-hole some 12 km south of Haditha (Widdowson 1954). There are many sink-holes in the area descending to the water table but the Sheik Hadid site differs from all the others in that it has a welling of water to the surface whereas the others are all land collapses of one kind or another. However, the presence of *Typhlogarra* in Widdowson's Pidgeon hole and in the Sheik Hadid well, strongly suggests that the same underground water system is involved. It is not known whether the underground system has any contact with the nearby Euphrates system.

At noon on 13 June 1979 the characteristics of the well water were: temperature 22° C; pH 7·5 and 0_2 content 1·5 mg l^{-1} and salinity 1·75 g l^{-1}. Although a detailed water analysis is provided later, the water may be summarised here as extemely hard, low in oxygen and salinity, and high in sulphates.

NOTES ON THE BIOLOGY. In addition to the two fish species, the underground waters support a yet undescribed species of the blind amphipod *Niphargus*. The stomachs of the post larval specimens of *Caecocypris* were empty but that of the larva contained a small piece of what seemed to be a chitinous material that may have come from an insect larva or a copepod. Dragonfly larvae, copepods, diatoms and green algae occur in the well if not in the completely lightless parts of the system. The blind fish have been seen to enter the well from all four openings and there they swim close to the pebbly bottom of the well. If disturbed they hide among the stones or swim back through the openings. They avoid being in the well when the light is bright and are most abundant at night. It is therefore likely that they are light sensitive to a limited degree.

On the basis of the collections made so far it seems that *Typhlogarra* is about twice as common as *Caecocypris* (68 cf 35). Mr Abdul Hameed Hasan has kindly informed us that the water temperature varies very little during the day or throughout the year, remaining between 21·5 and 22° C. He also observed that specimens less than a centimetre long are always present and concluded that the fishes breed throughout the year.

Both species are remarkably hardy, being able to endure considerable changes in water temperature and chemistry.

DIAGNOSIS. *Caecocypris basimi* can be distinguished from the sympatric *Typhlogarra widdowsoni* by the absence of barbels and mental disc. The former species has a large terminal mouth, the latter a small ventral mouth. *Caecocypris* is unique among cavernicolous cyprinids and middle eastern cyprinids in the possession of a free branchiostegal membrane.

AFFINITIES. In justifying the erection of a new genus for this species we indicated that no close relative could be found. Although *Caecocypris* possesses some undoubted apomorphies they seem to be autapomorphies rather than synapomorphies. As far as we have been able to discover the only other cyprinids with a free branchiostegal membrane are species of the genus *Hypophthalmichthys* from China. *Hypophthalmichthys* is highly derived and specialised for filter feeding (Fang 1928). It is tempting to suppose that the free branchiostegal membrane in *Hypophthalmichthys* is related to its feeding habits. Should that be so, it is unlikely that the free branchiostegal membrane in *Caecocypris* would serve the same function because, a) the species lacks the other modifications associated with filter feeding and b) it is unlikely that a cave system would afford it an adequate planktonic diet. The similar form of the branchiostegal membrane in these two genera therefore can only be interpreted as a parallelism.

The symphysial knob on the lower jaw is a character of mosaic distribution throughout the cyprinids. It occurs in some rasborines, chelines and aspinines (Howes 1978) and, more interestingly, in the cavernicolous, microphthalmic *Barbopsis devecchi* from Somalia. Other resemblance between *Barbopsis* and *Caecocypris* are similar body shape, large mouth, depressed head, similar meristic counts, two rows of pharyngeal teeth and a right-angled bend in the pharyngeal bone. However, the regressional trends associated with a hypogean habitat are not as advanced in *Barbopsis* as they are in *Caecocypris; Barbopsis* is eyed, pigmented, and has four barbels. (It should be noted that the ancestor of *Caecocypris* probably had barbels because the maxillary foramen for the innervation of the anterior barbel is still present although reduced. As far as we are aware, the maxillary foramen is invariably present in the members of that large group of 'barbelled' cyprinids as well as in members of the same group displaying secondary loss of barbels.). The branchiostegal membrane in *Barbopsis* is fused to the short, broad isthmus. We doubt, however, whether these similarities can be used as evidence for a postulated relationship. The body shape, depressed head, large mouth and similar meristics are all of such frequent occurence among the cyprinids as to nullify their use for this purpose. The right-angled bend in the pharyngeal bone could just as well be an obligatory response to similar head shapes as a synapomorphy. We have no precedents, nor evidence, to enable us to argue either case. Two rows of pharyngeal teeth (albeit with different numbers of teeth in the inner row) could indicate: a) reduction from three rows, a regressional trend noticed in other cavernicolous cyprinids e.g. *Caecobarbus* (Thines, 1969) and *Typhlogarra* (personal observation), b) the character was acquired independently or c) a synapomorphy. In view of the fact that so little is known about the polarity of trends associated with pharyngeal teeth we can have no confidence in using the number of rows of teeth to define relationships. Overall, because we cannot find any undoubted synapomophies for *Caecocypris* and *Barbopsis,* it can only be assumed that the similarities are due to parallelism.

No other Asiatic cave fish can be related to *Caecocypris.* Both *Typhlogarra* and *Iranocypris typhlops* are 'garrine' i.e. they have the mental disc, barbels and mouth structure characteristics of their epigean relatives in the genus *Garra.*

A search among the fishes of the Tigris and Euphrates has proved equally fruitless. We cannot find a species that we could postulate as the epigean relative of *Caecocypris.* In a way, this is no surprise. The general conservatism, coupled with the occasional small saltatory morphological changes, in cyprinid characters has the effect of making it difficult, if not impossible, to distinguish between parallelism and the sharing of characters derived through common ancestry. When these problems are overlain by the regressional trends associated with cave life, the likelihood of detecting the relatives of *Caecocypris* diminishes further.

Acknowledgements

It is with great pleasure that we acknowledge the help given to us by the following people and institutions. Dr P. H. Greenwood for his encouragement and his criticism of the manuscript. Mr Anthony Smith for his advice on the manuscript, for arousing interest in the caves of Iraq and for acting as courier for the living specimens of *Caecocypris.* Mr Abdul Hameed Hasan for putting his collection of Hadid fish at the disposal of M.K.B. The department of Chemistry and Minerals, Foundation General of Minerals (Iraq) for the detailed water analysis. The drawings of the holotype are the work of Mr Gordon Howes.

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Key to the abbreviations

A fin	Number of rays in the anal fin
C fin	Number of rays in the caudal fin
Cpl	Length of the caudal peduncle
Cpsc	Number of scales round the least circumference of the caudal peduncle
D	Greatest depth of the body
D fin	Number of rays in the dorsal fin
GR	Number of gill rakers on the lower limb of the first gill arch
HL	Head length, from the tip of the snout to the posterior extremity of the opercular bone
HW	Greatest width of the head
Ll	Number of scales in the mid-lateral line
MW	Greatest width of the mouth
P fin	Number of rays in the pectoral fin
S-D	Horizontal between a line perpendicular to the tip of the snout and the origin of the dorsal fin
SL	Standard length
V fin	Number of rays in the ventral fin
–	character absent
?	character unmeasurable or uncountable because of small size or damage.

All distances were measured with dial calipers.

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A new species of cichlid fish from the Malagarasi swamps and river (Tanzania, East Africa)

Peter Humphry Greenwood

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Introduction

The material described below was collected in the Malagarasi river and swamps by members of the East African Fisheries Research Organization (later the East African Freshwater Fisheries Research Organization) during a survey of the area carried out in August and September 1952. Details of the habitats from which specimens were obtained are given in Greenwood (1954:401–402).

The new taxon brings the total number of cichlid species recorded from the upper part of the Malagarasi system to six, of which five (the new species, *Astatoreochromis vanderhorsti* [Greenwood], *Orthochromis malagaraziensis* [David], *Sarotherodon karomo* [Poll], and *Serranochromis janus* Trewavas) are endemic; the sixth species, provisionally identified as *Astatotilapia bloyeti* (Sauv.), belongs to a poorly understood complex of taxa. It may well be specifically distinct from the type and other populations of *A. bloyeti*, and thus would also have to be considered an endemic of the Malagarasi system (see Greenwood, 1954, &1979:283–286, 297–298 and 302–303).

Astatotilapia paludinosa sp. nov.

Holotype. An adult male 100 + 26 mm long, from the Malagarasi swamps at Katare (Tanzania); BMNH reg. no. 1956.7.9.266.

The trivial name, from the Latin, refers to the nature of the type locality.

Description (Figs 1 & 2). Based on 56 specimens (including the holotype) from the Malagarasi swamps at and near Katare, and the river below Uvinza. The material is divided into two groups, one of fishes 20–50 mm standard length, the other of fishes from 52–108 mm SL.

Additional material, examined in the field, is incorporated in the colour descriptions and in the data on food and feeding habits.

In the table of proportions, head length, body depth and caudal peduncle length are expressed as percentages of standard length; all other measurements (indicated thus †) are given as percentages of head length. M = mean.

Standard Length	20–50 mm	52–108 mm
Depth of body	33·3–36·7 M = 34·8	33·4–40·1 M = 36·8
Length of head	33·3–38·3 M = 34·8	32·6–39·0 M = 35·0
Preorbital depth †	10·0–16·7 M = 13·2	14·0–19·0 M = 16·7
Interorbital width †	18·8–25·0 M = 21·3	18·2–24·0 M = 21·1
Snout length †	22·2–30·0 M = 26·4	28·0–33·3 M = 30·7
Eye diameter †	25·0–35·0 M = 30·2	23·5–30·9 M = 27·2
Cheek depth †	12·5–23·0 M = 19·4	22·8–28·5 M = 25·1
Caudal peduncle length	14·0–19·0 M = 15·8	11·5–16·4 M = 14·0

Dorsal head and snout profile straight, except for a slight interorbital concavity; sloping moderately steeply (*c.* 30°–35° to the horizontal). Snout as broad as or slightly broader than

Bull. Br. Mus. nat. Hist. (Zool.) **38** (3): 159–163

Issued 29 May 1980

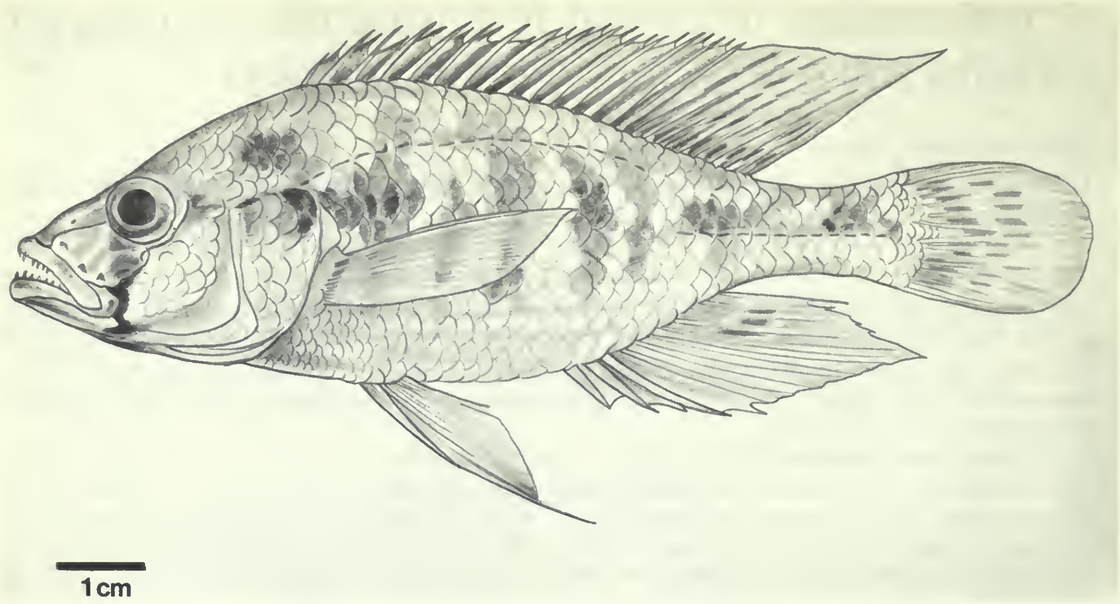

Fig. 1 *Astatotilapia paludinosa.* Holotype. Drawn by Gordon Howes.

long. Mouth slightly oblique; posterior maxillary tip extending to the vertical from the anterior orbital margin. Jaws equal anteriorly, the lower 33·3–46·0, M = 39·8 (fishes < 50 mm SL), and 38·0–44·5, M = 42·7 (fishes < 50 mm SL) per cent of head length; length/breadth ratio of the lower jaw 1·4–2·1 (mode 2·0).

Gill rakers. Short, 7–9 on the lower limb of the first arch, the lowermost one or two reduced.

Scales. Ctenoid except on the nape and chest; lateral line interrupted, with 29 (f.4), 30 (f.14), 31 (f.24), 32 (f.11) or 33 (f.3) scales. The last 2–6 scales of the upper lateral line series are separated from the dorsal fin base by 1 to $1\frac{1}{2}$ scales. Thoracic scales noticeably smaller than those occurring on the nape and belly. 7–10 (mode 9) scales between pectoral and pelvic fin bases; 5 or 6 (rarely 7) between dorsal fin origin and the upper lateral line. Cheek with 3 or 4 (mode), rarely 5 series of scales.

Fins. Dorsal with 24 (f.14), 25 (f.31), or 26 (f.11) rays, anal with 10 (f.1), 11 (f.24), 12 (f.28) or 13 (f.3) comprising XIV–XVI, 9–11 and III, 7–10 spinous and soft rays for the fins respectively. First pelvic ray produced, reaching to the vent in small fishes and as far as the third anal spine in larger individuals. Pectoral fin shorter than the head, 22·7–29·2, M = 25·7 per cent of standard length. Caudal moderately rounded.

Teeth. Outer series. In fishes between 21 and 70 mm SL, the majority of teeth in this series of both jaws are compressed and unequally bicuspid; individuals in the size range 77–95 mm SL have some unicuspid, caniniform teeth, chiefly in the lower jaw and posterolaterally in the upper. Above this size, moderately slender caniniform teeth predominate in both jaws. Tooth number is variable, but shows positive correlation with size; thus, fishes less than 45 mm SL have from 24–36 outer teeth in the upper jaw; in larger fishes the range is from 40–56 (one exceptional individual possessed only 32).

In fishes less than 70 mm SL, the posterior few teeth in the premaxillary outer series are not noticeably enlarged, nor are they unicuspid (the usual condition in most specimens of *Astatotilapia* species in the size range above 40 mm SL). Larger specimens, however, have the posterior 1–4 outer teeth larger than those preceding them, and invariably unicuspid.

Inner series. In fishes less than 90 mm SL, inner teeth are mostly tricuspid, but in larger individuals unicuspid teeth predominate, although an admixture of both types is common.

The number of inner rows in either jaw is variable, from 1–3, with 2 rows as the modal frequency at all sizes.

Lower pharyngeal bone (Fig. 2). Triangular, its dentigerous surface slightly broader than long (most fishes < 90 mm SL) or equilateral (fishes > 90 mm SL), its teeth arranged in 20–22 rows. Teeth of the median rows enlarged and stout, clearly cuspidate in small individuals, becoming conical and sub-molariform in the largest specimens.

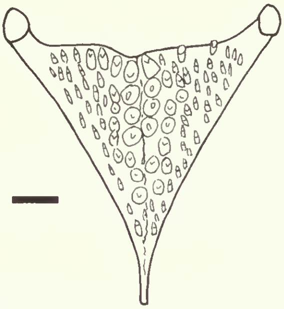

Fig. 2 *Astatotilapia paludinosa.* Lower pharyngeal bone; occlusal view (scale = 2 mm).

Skeleton. The neurocranium and jaw skeleton are identical with those in other *Astatotilapia* species (see Greenwood, 1979:274, 282 and fig. 6).

Vertebrae (excluding the fused PU_1 and U_1 elements) 28–30 (mode 29), comprising 12 or 13 (mode) precaudal and 15 or 16 (mode) caudal elements. The caudal fin skeleton in 21 of the 23 specimens examined radiographically has all the hypural elements free; in the two exceptional fishes hypurals 3 and 4 are fused.

Coloration. Preserved material. Since coloration of the few females caught is not markedly different from that of males, the description is applicable to both sexes. Ground colour brownish; seven to nine dark transverse bars on the flank and caudal peduncle, with faint indications of an interrupted mid-lateral stripe. A broad and distinct sub-lachrymal stripe is usually present. Posterior spinous and entire soft part of the dorsal fin maculate, less so in females; caudal fin maculate, especially on its dorsal half. Pectoral and anal fins clear, the latter, in males, with a single row of 3 or 4 ocelli with a narrow clear surround. Pelvic fins clear, or the outer half black, the leading edge of the first ray whitish.

Live coloration – breeding males. Ground colour grey-green; chest and belly dark silver-grey. Operculum golden; branchiostegal membrane blue-grey between the rami of the lower jaw, but yellow between the opercula. Lips iridescent blue. Dorsal fin yellow, lappets and margin red; dark red spots, often coalesced, on posterior spinous and entire soft part. Caudal fin with yellow lower and clear upper half on which deep-red maculae occur. Anal fin light grey, with a faint red flush; ocelli orange-yellow. Pelvics with outer half dusky, inner half yellowish; first ray blue.

Transverse and longitudinal banding was observed in live fishes, especially in a male seen guarding an established territory.

No information is available on the coloration of females.

ECOLOGY. *Distribution.* Lower Malagarasi river and swamps (Tanzania).

Habitat. The species was collected both in the swamp and the open river, at Katare and Uvinza respectively. At Katare, specimens were obtained from traps set amongst marginal vegetation, in open-water further off-shore and in nets set amongst dense off-shore stands of water-lilies. The greatest depth of water in any habitat was about 4 metres. A number of young *A. paludinosa* was found in a small and shallow pool partially isolated from the main swamp.

In the open river at Uvinza specimens were caught within the marginal reed beds, in the river itself and in sheltered embayments with a dense surface cover of water-lily leaves.

There appears to be no difference between the preferred habitats of this species and those of *A. bloyeti* inhabiting the same areas of the Malagarasi swamps and river. However, in the river at Uvinza *A. bloyeti* were relatively uncommon in areas away from the banks.

FOOD AND FEEDING HABITS. Analyses of stomach and intestinal contents in forty fishes (size range 44–107 mm SL) from all habitats at both localities provided little concrete evidence on the food of *A. paludinosa;* they do, however, indicate that the species is a bottom feeder.

In both the swamp area and in sheltered river embayments the bottom is largely covered by a thick deposit of semi-decomposed plant material. Detritus typical of this deposit was predominant in the stomach contents of twenty-five individuals. Since many of its constituents were partly decomposed before ingestion it is impossible to determine what material, if any, was digested by the fishes.

That the feeding habits of *A. paludinosa* are facultative is suggested by the occurrence of fish-guts as well as bottom debris in the stomachs of eleven individuals caught near a site where commercial catches were cleaned. Analyses made in the field showed that over 80% of fishes from this station had fed on fish offal. Scales and fish ova found in these fishes should probably be attributed to the same source.

Although some insect remains (Trichoptera, Ephemeroptera and Odonata larvae, and chironomid pupae) were recorded, insects, at least on the basis of this sample, do not contribute significantly to the diet of *A. paludinosa.*

Apparently there is little difference between the feeding habits of *A. paludinosa* and syntopic individuals of *A. bloyeti,* except that 21 of the 47 *A. bloyeti* specimens examined had ingested (and partly digested) water-lily seeds.

BREEDING. No data were obtained on breeding sites or habits, save for a single male seen guarding a 'nest' prepared in the sand substrate near emergent reeds. Sexually active fishes of both sexes were found in all habitats. Fishes less than 60 mm SL are sexually immature.

DIAGNOSIS. *Astatotilapia paludinosa* is distinguished from most congeneric species by its small chest scales (which are markedly smaller than those on the ventrolateral aspects of the flanks and belly, but are not separated from them by an abrupt change in scale size; see Greenwood, 1979), and, where live coloration is known, by its coloration and colour patterns (i.e. from *A. flaviijosephi* [Lortet], *A. nubila* [Blgr.], the *A. bloyeti* complex, *A. burtoni* [Günther], *A. swynnertoni* [Blgr.], *A. calliptera* [Günther] and *A. stappersi* [Poll]).

From the four *Astatotilapia* species with small chest scales, *A. paludinosa* is distinguished as follows:

(i) From *A. flaviijosephi* by its finer lower pharyngeal bone and few, less extensively molarized lower pharyngeal teeth (for a description of male coloration in *A. flaviijosephi* see Werner, 1976).

(ii) From *A. desfontainesi* (Lacép.) by its more slender head, especially its narrower snout (snout noticeably broader than long in *A. desfontainesi,* slightly longer than broad or, rarely, slightly broader than long in *A. paludinosa*), straighter, less decurved dorsal head profile, finer lower pharyngeal bone, and by its coloration, especially that of adult males (see Kirchshoffer, 1953, for colour descriptions of *A. desfontainesi*).

(iii) From *A. calliptera* by its smaller chest scales and in having outer row jaw teeth with acutely and unequally bicuspid crowns (as opposed to subequally bicuspid, obliquely truncate crowns in *A. calliptera*). Similar dental differences distinguish *A. paludinosa* from *A. swynnertoni,* which species also has relatively larger chest scales. Colour descriptions for *A. calliptera* and *A. swynnertoni* have been published by Bell-Cross (1976) and Jubb (1967) for the species respectively (the latter author treating *swynnertoni* as a synonym of *calliptera;* but see Greenwood, 1979:284).

(iv) From *A. dolorosa* (Trewavas) by its narrower interorbital width (18·2–24·0, mean 21·1% head length, cf. 25·8%), shallower cheek (22·8–28·5, mean 25·1% head length, cf. 30·3%) and its shorter, broader, lower jaw (38·0–44·5, mean 42·7% head length, cf. 48·6%; length-breadth ratio 1·4–2·1, mode 2·0, cf. 2·5 in *A. dolorosa*). All these morphometric comparisons are with *A. paludinosa* in the size range 52–108 mm SL; the holotype and unique specimen of *A. dolorosa* is 93·5 mm SL. For further comments on these two species see below.

AFFINITIES. The small chest scales of *A. paludinosa,* apparently a derived character (see Greenwood, 1979:270–271), suggest that the species' closest living relatives are *A. desfontainesi* (Tunisia and Algeria), *A. flaviijosephi* (Israel and Syria) and *A. dolorosa* (Lake Edward basin, Uganda).

In its overall morphology, particularly its more streamlined head shape, *A. paludinosa* resembles *A. dolorosa* more closely than it does the other two species, but the phylogenetic significance of that feature cannot be assessed; it would certainly seem to be the commonest form amongst the African *Astatotilapia* species, and thus may be the primitive condition.

The extent to which the lower pharyngeal bone and its dentition are hypertrophied (presumably a derived feature) suggests that *A. flaviijosephi* and *A. desfontainesi* are more closely related to one another than to any other *Astatotilapia* species. As a corollary, the finer bone and dentition found in *A. paludinosa* and *A. dolorosa* is probably a feature of little phylogenetic significance.

Unfortunately *A. dolorosa* is known only from the holotype, a specimen now rather flaccid and completely bleached of its body and fin markings. This fish differs from comparable-sized *A. paludinosa* in certain morphometric features (see under Diagnosis above), which, since they involve bony features are not likely to be affected by the relatively poor condition of the specimen. However, the importance of the features in helping to establish the affinities of *A. paludinosa* are diminished by the absence of other *A. dolorosa* specimens. No further material of that species has been captured, despite recent collections made in the vicinity of the type locality.

Clearly the relationships of *A. paludinosa* cannot yet be determined. It is, however, interesting to note that they do not appear to lie with congeners presently occurring in the same geographical area (Lake Tanganyika basin and drainage), that is *A. burtoni,* the *A. bloyeti* complex, or *A. stappersi.*

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. no.	Locality	Collector
BM(NH) 1956.7.9.266 (Holotype)	Katare, Malagarasi swamps.	E.A.F.R.O.
BM(NH) 1956.7.9.267–285 (Paratypes)	Katare, Malagarasi swamps.	E.A.F.R.O.
BM(NH) 1956.7.9.291–311 (Paratypes)	Katare, Malagarasi swamps.	E.A.F.R.O.
BM(NH) 1956.7.9.254–265 (Paratypes)	Malagarasi river at Uvinza (below the rapids).	E.A.F.R.O.

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A new catfish from Sierra Leone

Gordon Jon Howes

Zoology Department, British Museum (Natural History), Cromwell Road, London SW7 5BD

A collection of freshwater fishes from Sierra Leone made by Dr A. I. Payne contained three specimens of a previously undescribed dwarf catfish. At first sight these small fishes (33·5–36 mm SL) were thought to be the juveniles of a *Synodontis* species, but closer examination showed many significant differences. Furthermore, dissection of two specimens revealed that they were adult females, having ripe ovaries. In overall morphology the new catfish appears closer to members of the Mochokidae *sensu lato* than to those of any other siluroid family, (see p. 168). The possibility that these fishes belonged to the dwarf mochokid genus *Microsynodontis* was dispelled when comparisons were made with species of that genus.

MOCHOKIELLA gen. nov.

Fishes of a small size with a shallow body (depth 25·5–27·9 of SL). Head broad (almost equal to its length) with dorsal profile sloped, snout rounded, ethmoid with narrow rostral process. Nostrils widely separated, the posterior situated midway between the anterior nostril and the orbital rim. Anterior nostril tubular. Mouth small, lower lip developed only at the corners of the mouth. Premaxillary teeth short and conical, in a broad patch. Dentary teeth like those on the premaxilla, set in a broad semi-crescentic band. Vomerine teeth absent. One pair of maxillary and two pairs of mandibular barbels. The maxillary barbel long, reaching to the tip of the cleithral process. Outer mandibular barbel extending to halfway along the cleithral process, the inner reaching to the base of the pectoral spine. The outer barbel bears 3 long branches, or sub-barbels, and the inner has 4 (number constant in all specimens). The nuchal shield is well-developed, slightly rugose. There are 3 nuchal plates, the 3rd paired, divided by the 1st and 2nd dorsal fin spines. The cleithral process is narrowly triangular, extending to a line level with the edge of the 3rd nuchal plate.

Eye supero-lateral without free orbital rim. Pectoral spine strong, almost reaching the origin of the pelvic fin, its anterior margin bears 23 serrations, the posterior margin 8–9 strong 'teeth'. The longest ray of the pelvic fin reaches to the origin of the anal fin. Anal fin base short, as long as the caudal peduncle. Adipose fin deep and long based, equal to its distance from the last dorsal fin ray. Caudal fin long and forked. Branchiostegal rays 6. Gill opening extending to the base of the pectoral fin spine; branchiostegal membrane forming a fold across the ventral surface of the head. Gill-rakers small, 6 on 1st ceratobranchial. Lateral line pores prominent, interrupted.

Mochokiella is distinguished from all other African siluroids by a combination of characters including small adult size, uni-lateral branching of the mandibular barbels, supero-lateral position of the eye, bands of villiform jaw teeth, elongate humeral process, paired 3rd nuchal plate and distinctive colouration (see below).

Type species: ***Mochokiella paynei*** sp. nov

(Fig. 1)

Holotype. An adult female, 33·5 mm SL BMNH 1979.8.22:1 collected from Kassawe Forest Reserve, Sierra Leone by Dr A. I. Payne, for whom the species is named.

Description. Based on the holotype and two paratypes, BMNH 1979.8.22:2–3, 35·5 & 36 mm SL. Characters given here amplify the preceding generic description. The proportions given below are shown as percentages of the standard length except for nos

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	Holotype 1979.8.22 : 1	Paratypes 1979.8.22 : 2-3	
Standard length	33·5 mm	35·5 mm	36 mm
Depth	27·0	25·5	27·9
Head length	31·5	31·5	29·2
Interorbital width	38·0	40·0	38·0
Snout – dorsal fin	39·0	39·5	39·0
Eye diam.	19·0	22·5	24·0
Mouth width	27·0	28·5	28·5
Head width	30·0	31·0	29·2
Snout length	38·0	40·0	43·0
Maxillary barbel	132·0	130·0	119·0
Mandibular barbel, outer	105·0	112·0	105·0
Mandibular barbel, inner	76·0	71·0	67·0
Cleithral process length	15·4	18·4	19·4
Cleithral process depth	28·2	31·0	23·0
Pectoral spine length	27·0	24·0	27·9
Pelvic spine length	12·0	12·6	12·5
Dorsal spine length	22·5	22·5	22·1
Dorsal – adipose distance	26·9	34·2	22·1
Adipose fin length	26·9	24·0	19·4
Caudal peduncle length	13·4	15·5	11·1
Caudal peduncle depth	12·0	11·3	9·7
Anal fin base length	14·0	12·7	16·6
Dorsal fin rays	II6	II6	II6
Pectoral fin rays	I6	I6	I6
Pelvic fin rays	I6	I6	I6
Anal fin rays	I10	I9	I10
Gill-rakers on lower arch	6	Unknown	Unknown
Vertebrae excluding fused anterior elements	27	27	27

3,5,6,8–11, which are percentages of the head length; the depth of the cleithral process (13) is shown as a percentage of its length (12).

COLORATION. The overall body colour pattern is mottled, the top of the head dark with indistinct transverse bands. A dark band links the nostrils to the eye and a diffuse band runs antero-ventrally from the eye to the mouth. A light stripe crosses the interorbital space. The cheeks and operculum bear dark patches. A distinct dark band runs across the supraoccipital, and is followed by a broad light patch and then another dark band on each 3rd nuchal plate, which are divided by the dorsal fin. From the base of the dorsal fin to the mid-lateral line is an area of dark brown pigment. Below the cleithral process this pigment is broken into a reticulated pattern. Just above the pelvic fin is a dark, irregular patch encircled by a light band. An extension of this band continues dorsad to meet its partner and form a light area anterior to the adipose fin. In the paratypes the mid-lateral blotch is much less distinct than in the holotype, the encircling band being broken and interrupted mid-dorsally. From the rear of the adipose fin a broad light stripe runs down to the posterior part of the anal fin. The dorsal part of the caudal peduncle is uniformly dark; below the lateral line is a lighter coloured spot just posterior to the anal fin, followed by a darker patch at the base of the caudal fin. Again, on the paratypes these markings are less distinct and more reticulated. In all specimens the ventral surface of the body is mottled with light brown pigment, a small darker patch occurs at the base of each pelvic fin.

The adipose fin is mostly dark, but with a light posterior margin. In one of the paratypes the posterior tip has a distinct spot, and in the other there are two spots. All other fins are barred and blotched. All barbels are barred.

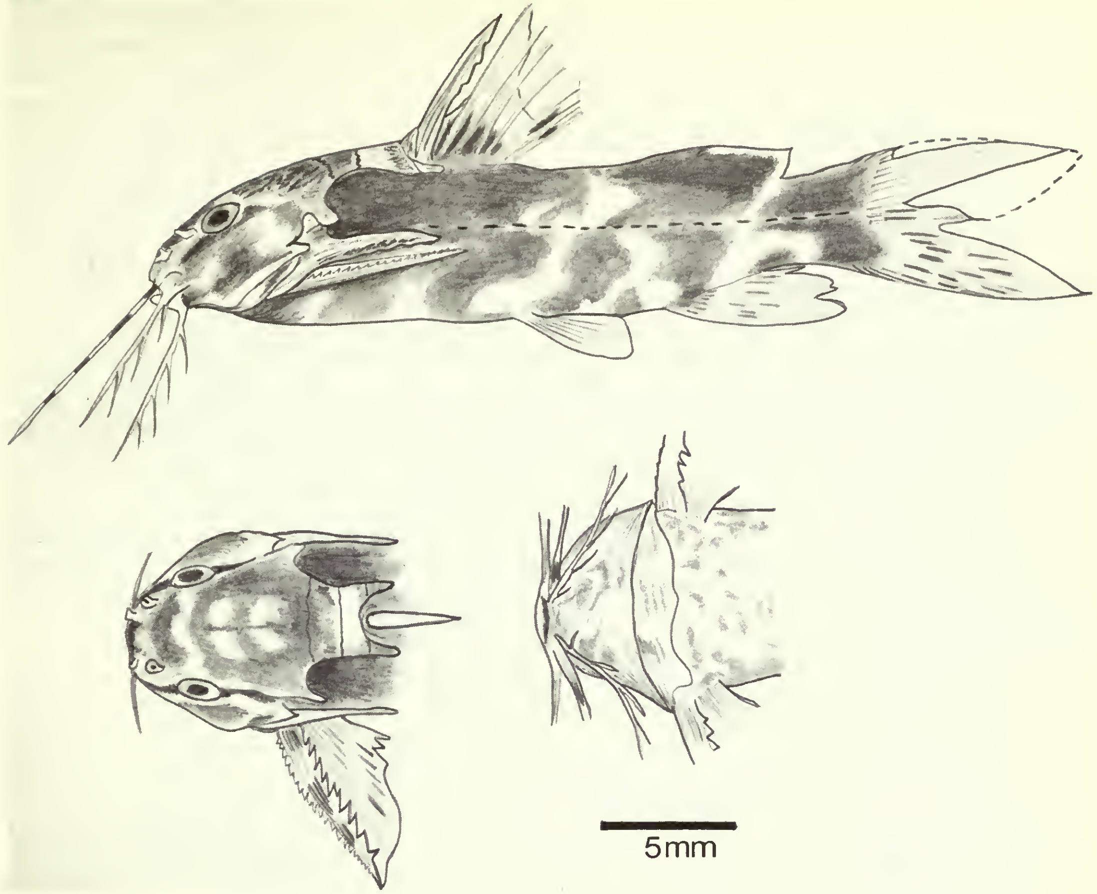

Fig. 1 *Mochokiella paynei;* above, lateral view; below, dorsal and ventral views of the head.

Life colours have been recorded from 6 imported aquarium specimens: The light areas are cream to beige and the dark areas Vandyke Brown. The markings on the head are more distinctive and appear as individual blotches and spots. The patterning differed little from that of the types, most noticeable was the variation in the markings of the adipose fin. However, the main features – the pale nuchal band, striped snout, mid-lateral reticulation and caudal peduncle band were well-developed.

HABITAT AND HABITS. The type locality is a forest stream in Kassewe Forest Reserve with a pH of 6·6. The fish were caught overnight in a baited trap.

Recent trade aquarium imports from Sierra Leone have included specimens of *Mochokiella paynei,* and six individuals have been observed in aquaria. The fishes readily seek shelter in cavities provided by rocks and wood; sometimes swimming vertically or upside-down against the cavity walls. They are most active at night, moving outside their hiding places. One fish was seen resting along an almost upright plant stem, supported by its caudal fin. All known aquarium specimens have been of the same or slightly larger size than the type series. Of the type specimens, two have ovaries each containing a total of *c.* 30 eggs.

PHYLOGENETIC RELATIONSHIPS. Both the lack of osteological material of *Mochokiella* and knowledge of the distribution of certain anatomical characters throughout the Siluroidei makes any judgement of the taxon's relationships highly speculative.

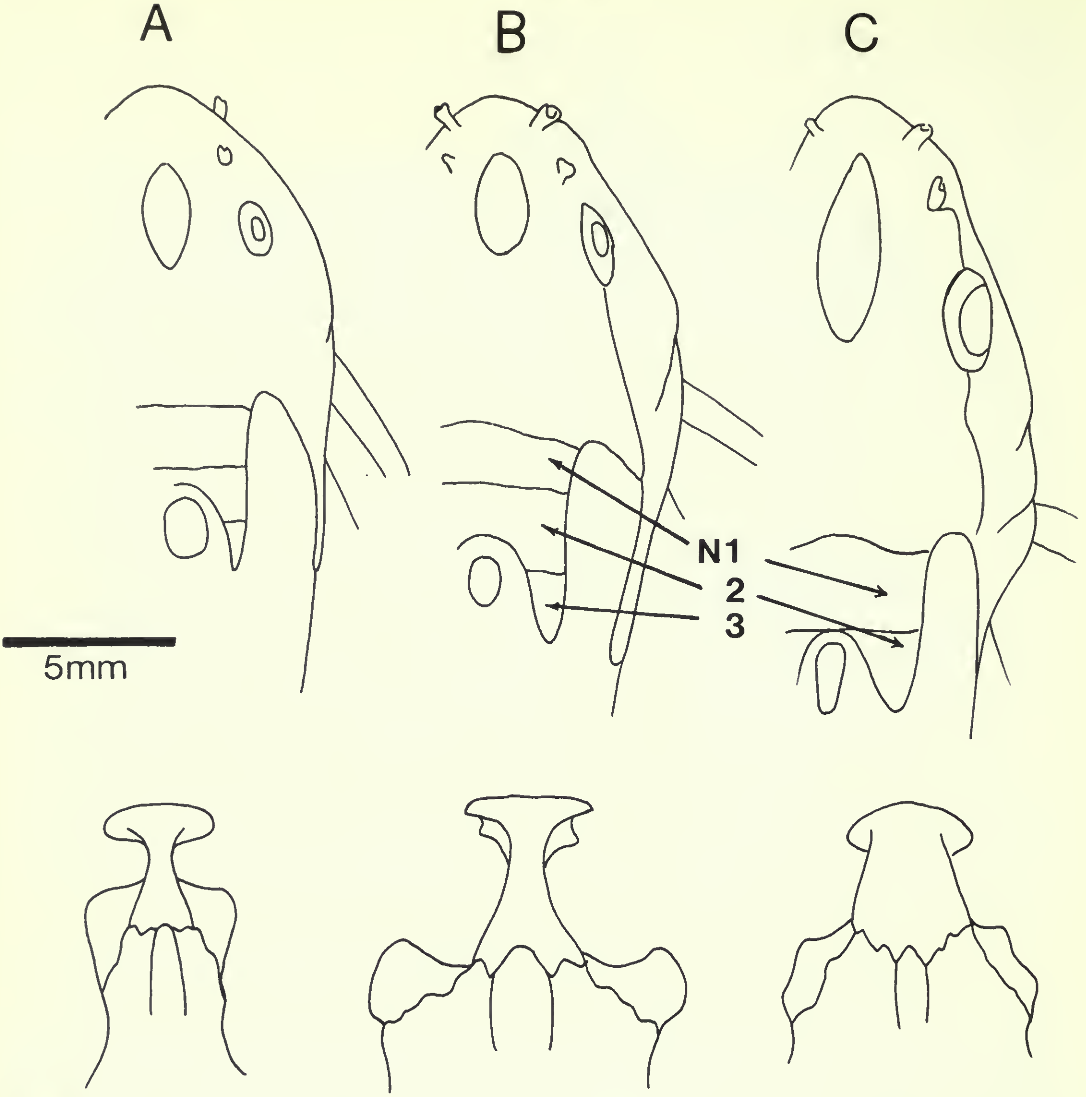

Fig. 2 Dorsal views of the heads and ethmoid regions of A. *microsynodontis batesii,* B. *Mochokiella paynei,* C. *Synodontis melanopterus.* All specimens are of the same size, 36 mm SL. N1,2 & 3 = nuchal plates.

Assignment to the Mochokidae is made solely on the grounds of superficial resemblance and must be viewed as a temporary expedient (see below). Character comparison of *Mochokiella* with *Microsynodontis* and *Synodontis* is given below and in Fig. 2.

On the basis of more numerous similarities, *Mochokiella* more closely resembles *Microsynodontis* than any other mochokid. Present lack of data makes it impossible to say whether these similarities are to be regarded as based on apomorph or plesiomorph features. The ethmoid of both *Mochokiella* and *Microsynodontis* is long and narrow, in contrast to the broad, thick ethmoid of other mochokids (Figs 2A & B), the only exception being *Mochokus.* A similarly elongate ethmoid occurs in some bagrids, e.g. *Chrysichthys* and *Auchenoglanis.* Research on other otophysans – characoids and cyprinoids – has indicated that an elongate ethmoid is an apomorph character. However, it should be noted that an elongate ethmoid is present in *Diplomystes,* considered by some authors as a primitive siluroid (Regan, 1911;

Alexander, 1966). *Mochokiella* shares with *Microsynodontis* and *Mochokus* two other features. One is the elongate posterior cleithral process (humeral process) which is short and broadly triangular in other mochokids and bagrids. The other character is the number and form of the nuchal plates, there being 3 in all three genera, the 2nd partially divided by the dorsal fin spine and the 3rd completely divided. In other mochokids and amphiliids there are two nuchal plates (see Taverne & Aloulou-Triki, 1974). *Mochokiella* has the parapophyses of the 4th and 5th vertebrae well-developed, spine-like and extended laterally as in *Synodontis.* In *Mochokus* these parapophyses extend upward to contact the ventral surface of the nuchal plates and in *Microsynodontis* they contact each other laterally to form a continuous shelf – similar to that illustrated for *Pimelodus* by Alexander (1966).

The dentition of *Mochokiella* is distinctly different from that of other mochokids, and it more closely resembles that of bagrids. However, this is most likely to be a plesiomorph rather than an apomorph character.

Mochokiella differs from other species of *Microsynodontis* in having greater body depth, longer head, greater interorbital width, longer snout to dorsal distance, larger eye, longer mandibular barbels, longer dorsal and pectoral spines and caudal fin forked instead of rounded.

	Mochokiella	*Microsynodontis*	*Synodontis*
Nuchal plates	3	3	3
Ethmoid	elongate	elongate	short and broad
Eyes	small, superolateral; no free orbital rim	Minute, superior; no free orbital rim	large, lateral or supero-lateral; free orbital rim
Lower lip	weak	well-developed	usually well-developed
Dentary teeth	small, conical, all of equal size set in broad band	slender, hook-like, the outer row longer than the inner, set in narrow band	elongate, hook-like, outer row longer than the inner, set in small, rounded patch
Premaxillary teeth	small, conical, all of equal size set in broad patch *c.*45 on each pmx.	slender, elongate set in broad patch *c.* 45–50	stout, elongate set in narrow band, *c.* 30
Mandibular barbels	with thin sub-barbels	with thick sub-barbels	with numerous sub-barbels sometimes tuberculate
Gill opening	extending anterior to pectoral base	to pectoral base	to pectoral base
Branchiostegal membrane	transverse ventral fold	transverse fold	fold lacking
Pectoral fin spine	anterior serrations, 25–26	28	28–29
Lateral line	interrupted	interrupted	complete
Adipose fin	long	short	variable
Cleithral process	elongate	elongate	broadly triangular
Caudal fin	forked	rounded	forked

As currently recognized, the Mochokidae contains the genera *Mochokus, Microsynodontis, Atopocheilus, Acanthocleithrum, Chiloglanis, Euchilichthys, Synodontis, Hemisynodontis* and *Brachysynodontis.* Taverne & Aloulou-Triki (1974) recognized the diverse nature of this family by placing the latter three genera into the subfamily Simuldentinae. Although these authors listed a set of characters defining the subfamily, no comparison was made with the other non-included genera nor with other siluroids, Thus, the distribution of these characters within the suborder is unknown. From preliminary observations of the osteology of the Mochokidae I would venture to suggest that the family is possibly polyphyletic.

Acknowledgements

My most sincere thanks are due to Dr A. I. Payne for collecting the catfishes and providing habitat information, and to Stephen Pritchard who first drew my attention to aquarium imports and provided not only data on the habits of live fishes but with the singular osteological preparation of the species. I am most grateful also to Mr & Mrs D. Lambourne for their notes on live specimens.

I am indebted to Dr Max Poll, formerly of the Musée Royal de l'Afrique Centrale, Tervuren for loaning the holotype of *Microsynodontis polli* and to Dr P. H. Greenwood for commenting on the manuscript.

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A new genus of cheline cyprinid fishes

Gordon Jon Howes

Zoology Department, British Museum (Natural History), Cromwell Road, London SW7 5BD

In a recent review of the cyprinid genus *Barilus* (Howes, 1980), it was noted that one species, *Barilius auropurpureus* Annandale, 1919 was not a member of that genus but that it shared derived characters with the cheline group of cyprinids. This paper amplifies that statement and establishes a new genus to contain the species.

Annandale (1918) described *Barilius auropurpureus* from Inle lake basin, south Shan States in Burma. He did not, however, compare the species with any other *Barilius* and gave no reason for including it in that genus. I have examined a series of specimens collected by Annandale and can find no characters that indicate affinity with *Barilius* or any member of the bariliine group (*sensu* Howes, 1980). On the contrary, *auropurpureus* shares apomorph features with the cheline group (*sensu* Howes, 1979). These characters are: marginal overlap of the supraethmoid by the frontals; triangular, lamellate kinethmoid; ethmo-vomerine bloc extended anteriorly and laterally as a shelf; wide midline separation of the medial anterior maxillary processes; anteriorly notched and hooked dentary; truncated supraoccipital; long, posteriorly curved lateral processes on the 2nd vertebra.

Inclusion of *auropurpureus* in an existing cheline genus is precluded on the grounds of its autapomorphic features involving the ethmoid and jaw morphology (see below). I propose therefore that *'Barilius' auropurpureus* be assigned to a new genus:

INLECYPRIS gen nov.

TYPE SPECIES. *Barilius auropurpureus* Annandale, 1918

Slender fishes with large eye, pointed snout and obliquely angled mouth; ventral keel present. Supraethmoid produced laterally, the mesethmoid extending anteriorly beyond the supraethmoid as a shelf; preethmoid minute; kinethmoid lamellate, triangular; symphysial notch and process on dentary; large nasal; infraorbitals well developed, the 5th small and contacting the wide supraorbital; frontals narrow, overlapping the posterior margin of the supraethmoid; dilatator fossa small; parasphenoid horizontal, separated from the orbitosphenoid by a shallow septum; minute metapterygoid-quadrate fenestra; vertical cleithral limb short; postcleithrum well-developed, curved mesad; coracoids meeting along their ventral margins; neural complex low; 7 large lamellate supraneurals – 1st & 2nd fused; lateral processes of 1st and 2nd vertebrae elongate and caudally directed; total number of vertebrae 37 (4+10+22+1).

A single species, *Inlecypris auropurpureus* (Annandale, 1918), known only from Inle lake basin, Burma. Annandale (1918; 1922) adequately described the species, its habitat and habits.

RELATIONSHIPS. Within the cheline group *Inlecypris* shares derived characters with *Chela*. The ethmoid region of both taxa is very similar. The supraethmoid is overlapped posteriorly by the frontals, the mesethmoid is depressed and is produced anteriorly as a long shelf, the preethmoids are minute. Both genera have a flat, triangular kinethmoid (Figs 1 A & B). Other synapomorphic features are the enlarged nasal; the morphology of the upper jaw, which in *Chela* lacks a prominent mid-lateral maxillary ascending process and which in *Inlecypris* is reduced to a spine (cf. Figs 2A & B); the posterior curvature of the cranium, reduction of the supraoccipital process and absence of posttemporal fossae; morphology of the supraneurals; morphology and degree of development of the transverse processes on the 1st and 2nd vertebrae. Both taxa also possess an enlarged supracleithrum which covers the

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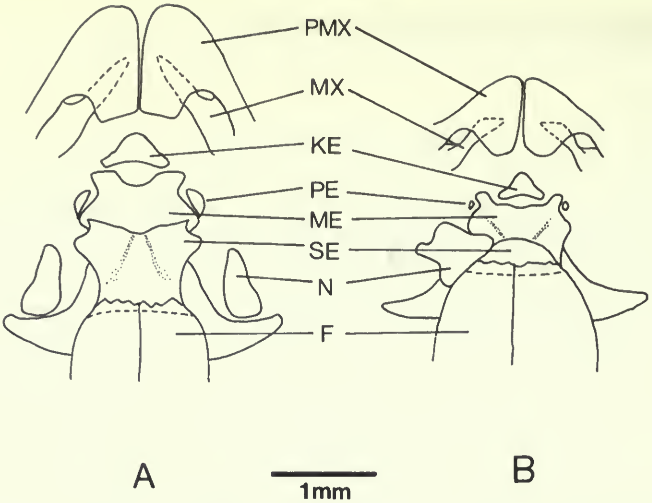

Fig. 1 Dorsal views of the ethmoid regions of A, *Inlecypris auropurpureus* and B, *Chela laubuca*. F, frontal; KE, kinethmoid; ME, mesethmoid; MX, maxilla; N, nasal; PE, preethmoid; PMX, premaxilla; SE, supraethmoid.

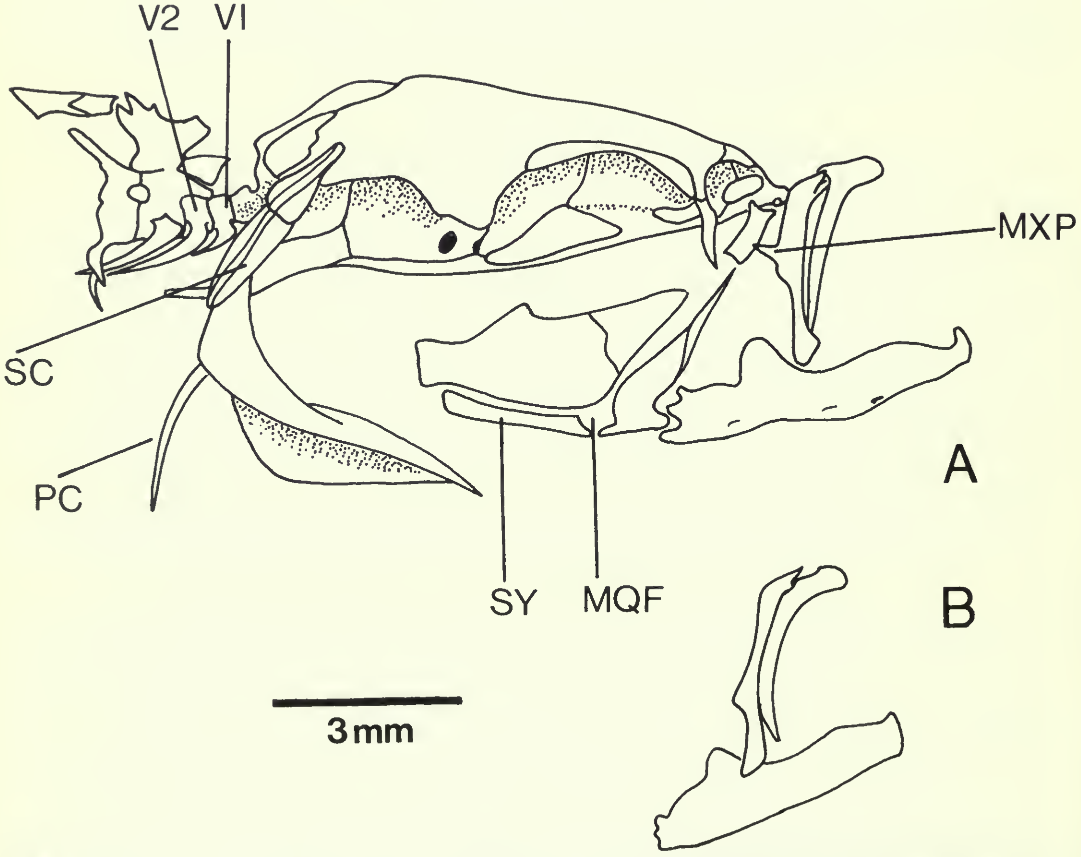

Fig. 2 A. *Inlecypris auropurpureus,* lateral view of the neurocranium with jaws, part of suspensorium, pectoral girdle and vertebral column in articulation. B. *Chela laubuca,* lateral view of jaws. MQP, metapterygoid-quadrate fenestra; MXP, mid-lateral maxillary process; PC, postcleithrum; SC, supracleithrum; SY, symplectic; V1 & 2, 1st and 2nd vertebrae.

upper half of the cleithrum (cf. Fig 2A with Fig 35 in Howes, 1979). The form of the lower jaw in *Inlecypris* more closely resembles that of other members of the cheline group *viz Oxygaster* and *Salmostoma.*

Howes (1979) recognizes three lineages within the cheline group, the cheline lineage being represented solely by the genus *Chela.* Some modification to this classification is now required. *Chela* undoubtedly displays greater cranial and vertebral modifications than does *Inlecypris* (Howes, 1979). The absence in *Chela* of a symphysial notch and midlateral maxillary ascending process are possibly to be regarded as secondary loss characters – the reductive trend being witnessed in *Inlecypris.* Thus, now *Chela* and *Inlecypris* comprise the cheline lineage which forms the sister group to the combined assemblage of salmostomine and oxygastrine lineages (see cladogram in Howes, 1979).

Writing of the ichthyofauna of the Inle basin, Annandale (1918) noted that of the 17 recorded genera 2 were endemic (*Chaudhuria* (Chaudhuriidae) and *Sawbwa* (Cyprinidae)). *Sawbwa* is a minute, scaleless cyprinid of unknown affinity. It does not possess cheline characters and may possibly belong to a subgroup of the rasborine complex. Annandale (1918) described another cyprinid genus, *Microrasbora,* represented by two species in the Inle basin, *M. rubescens* and *M. erythromicron.* He believed, however, that *Microrasbora* was widespread throughout the Malay Peninsula and that *Rasbora heteromorpha* Dunker, 1904 and *R. maculata* Dunker, 1904 should possibly be included in the genus. Paucity of specimens of *Microrasbora* prevents analysis of osteological characters but superficially its two contained species greatly resemble *Sawbwa* except that they are scaled. As in *Sawbwa* the ethmoid region is narrow and the lower jaw shallow; there is a patch of dark pigment surrounding the vent and the genital pore is enveloped in a thickened sheath. These characters are lacking in *Rasbora heteromorpha* and *R. maculata.*

Thus, it would appear that there are four endemic genera in the Inle basin. Of the cyprinids, *Inlecypris* is a relatively plesiomorph member of its lineage. Its closest relative, the more derived *Chela,* is widespread throughout the South-East Asian archipelego.

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A redescription of *Trochammina nana* (Brady) (Protozoa: Foraminiferida), with observations on several other Recent Trochamminidae in the Collections of the British Museum (Natural History)

P. Brönnimann

Laboratoire de Paléontologie, Université de Genève, 13, rue des Maraîchers, 1211-Genève-4, Switzerland

J. E. Whittaker

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Introduction

As part of a major revision of the Trochamminidae from several parts of the world, in particular the waters of the South Atlantic (Brönnimann, 1976, 1979; Brönnimann & Beurlan, 1977, 1977*a*; Brönnimann & Whittaker, in preparation), the present authors have found in necessary to examine the important Recent foraminiferal Collections of H. B. Brady and Heron-Allen & Earland, housed in the British Museum (Natural History) (B.M.N.H.). In the Brady Collection, several of the trochamminids have been found to be in need of taxonomic revisison, and this paper deals with the confusion surrounding *Haplophragmium nanum.*

Brady (1881 : 50) proposed for a small trochospiral agglutinated foraminifer collected by the *Challenger* Expedition, the name *Haplophragmium nanum.* At the time he did not specify the station(s) at which the new species occurred, and he described it, without illustration, as follows:

> 'Test minute, rotaliform, depressed; superior face somewhat convex; inferior, plane, more or less excavated at the umbilicus; margin rounded, lobulate. Consists of about two revolutions, each composed of about six inflated segments, often irregular in shape and disposition. Shell texture thin, resembling that of *H. canariense.* Diameter. 1/75 inch (0·34 mm).'

H. nanum Brady is therefore a valid name according to Article 12 of the International Code of Zoological Nomenclature. The lack of illustration is however unfortunate in the light of the ensuing taxonomic disorder.

Subsequently, Brady (1881*a*) reported *H. nanum* from Arctic waters. This was material from the Austro–Hungarian North Polar Expedition and had been sent to Brady for identification by his friend Dr F. Karrer of Vienna. Brady's text was translated into German and apart from one or two mis-translations and an extra plate (pl. 1) showing the locations of the soundings in the vicinity of Franz-Josef Land and Novaya Zemlya, is identical to the English text; the German version was not however published until 1882.

Haplophragmium nanum is said by Brady (1881*a*: 406) to be. . . 'the commonest of all the smaller arenaceous forms, over the whole area reported by these soundings . . .'.He also states that the Arctic specimens are . . . 'rather smaller than those described from the *Challenger* dredgings [Brady, 1881] and seldom exceed 0·25 millim. in diameter; they are generally less convex on the superior surface and altogether somewhat thinner . . .'. The

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accompanying illustration (Brady, 1881*a*, pl. 21, figs 1a–c) is apparently of a single specimen in spiral, edge and umbilical views, and is the first published figure. It must however be emphasized that this specimen was not from the *Challenger* material from which the original description was made.

In the *Challenger* Report, Brady (1884: 311, pl. 35, figs 6a–c, 7, 8) described *H. nanum* again in more detail, giving the locations of his figured specimens. That shown in plate 35, figs 6a–c appears at first glance to be identical to the specimen in plate 21, figs 1a–c of his 1881*a* paper, but on close examination can be seen to differ in several respects particularly in edge and umbilical views. Perhaps Brady had merely instructed his engraver, Mr Hollick, to make the previous illustration a little more accurate, or may have had drawn a completely different specimen. According to our records, the specimen shown in Brady, 1884, pl. 35, figs 6a–c, comes from a slide of about 40 individuals from the Austro–Hungarian North Polar Expedition station 518, off Franz-Josef Land (B.M.N.H. slide no. ZF 1546), at 113 fathoms (207 m), but it is not possible to ascertain with certainty which particular individual was figured. Brady did not himself designate holotypes nor in general give any indication as to which syntype(s) he illustrated. Nevertheless, this figured specimen is typical of the suite in ZF 1546. Figures 7, 8, of Brady's plate 35 were also attributed to *H. nanum* and came from *Challenger* station 346, north of Ascension Island in the South Atlantic (B.M.N.H. slide no. ZF 1547), at 2,350 fathoms (4,300 m). Two specimens were used for the engraving; only 8 syntypes now remain.

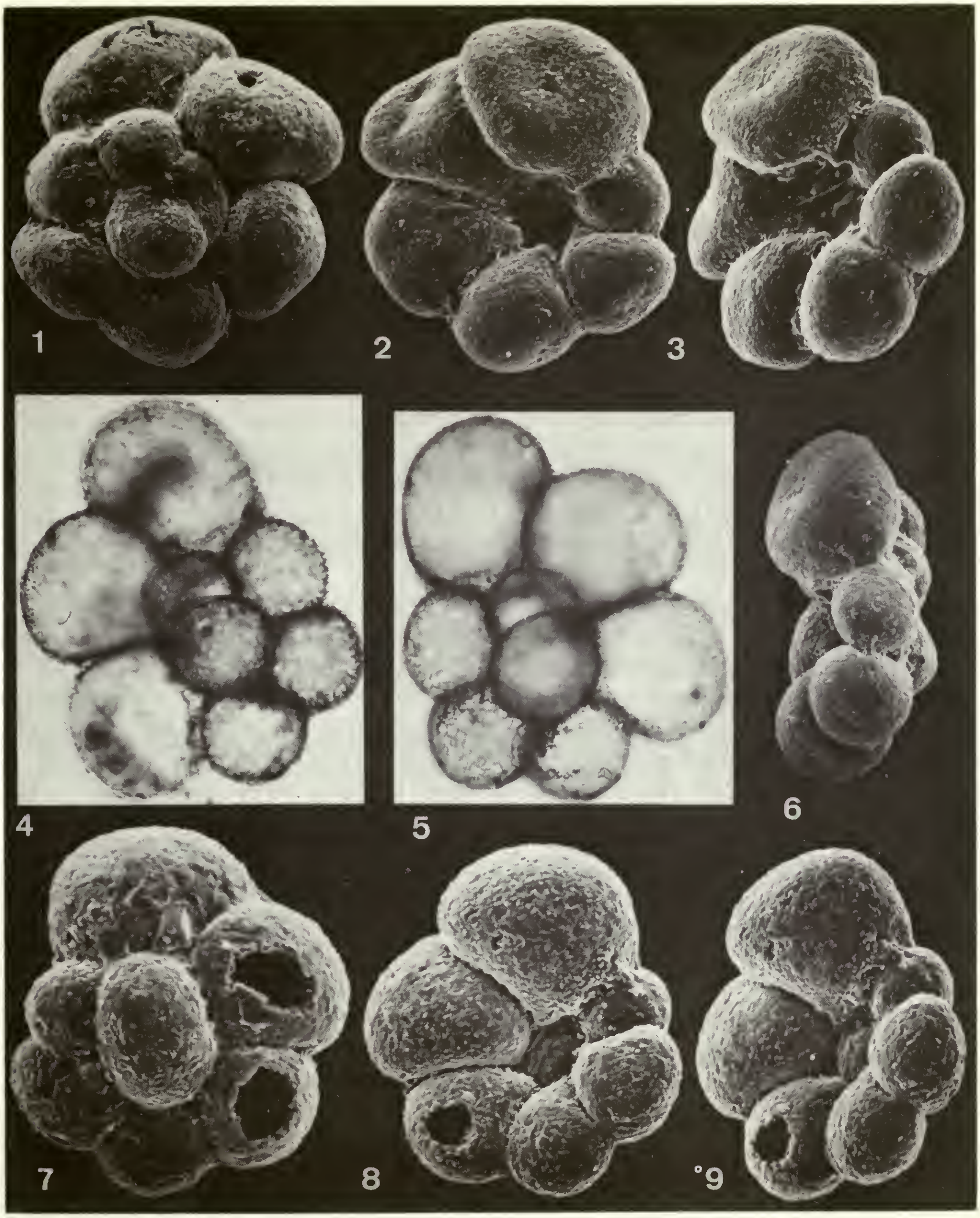
Brady (1884) was obviously of the opinion that the Arctic and South Atlantic forms were conspecific, but probably because he had seen many more specimens from the Austro–Hungarian North Polar Expedition dredgings than from the *Challenger*, he wrote that . . . (p. 312) . . . 'fig. 6 represents the typical form, while figs 7 and 8 are examples of irregularly grown tests'. Nevertheless, he felt it necessary to modify his original description to accommodate the Arctic forms . . .

> 'Test minute, Rotaliform, depressed; consisting of about two convolutions, the outermost of which is composed of six or seven somewhat inflated segments, often irregular in shape and disposition. Superior face flat or slightly convex; inferior face convex, more or less excavated at the umbilicus. Walls thin; texture resembling that of *Haplophragmium canariense*; colour light-brown, the final segment somewhat lighter than the rest. Diameter 1/75 inch (0·34 mm) or less.'

Subsequent workers (e.g. Barker, 1960) have always followed Brady (1884) and apart from referring it to *Trochammina,* have accepted this wide concept of the species without question. After studying the early literature on *H. nanum* outlined above, our growing apprehension that Brady had in fact confused two distinct species was confirmed on examining the respective syntypic slides in the Museum. It was also possible to produce scanning electron micrographs of several specimens from each slide and the results are illustrated in this paper. The two forms are shown not only to be separate species, but also to warrant separate generic status.

Haplophragmium nanum Brady must be based on the *Challenger* South Atlantic material from north of Ascension Island (Stn 346) as the first valid description (Brady, 1881) was made without reference to the Arctic collections (R. V. Melville, pers. comm.). The species is now redescribed and illustrated (Figs 1–9) as a *Trochammina* and a lectotype chosen. Specimens from the Austro–Hungarian North Polar Expedition stations, even though later stated by Brady (1884) to . . . 'represent the typical form . . .', must be given a new name; we propose *Portatrochammina bipolaris* sp. nov., as it has also been found to occur in Antarctic as well as Arctic waters (see Figs 15, 16, 18–31).

We have examined every one of the very many slides in the Collections labelled *Haplophragmium nanum* (or *Trochammina nana*), ranging in age from Cretaceous to Recent and from present day polar, temperate and tropical regions, in order to ascertain the true geographical and stratigraphical range of the species under review. This information is given in the Systematic part below (pp. 178–183). Of the slides in the Brady Collection attributed to *H. nanum,* several contain a further new species, not previously illustrated by



Figs 1–9 *Trochammina nana* (Brady). Figs 1–3, 6, Lectotype (ZF 3971); spiral, umbilical, oblique-umbilical and edge views. (Believed to be specimen illustrated by Brady, 1884, pl. 35, fig. 8), × 118. Figs 4, 5, Paralectotype (ZF 3972); umbilical and spiral views in immersion oil, × 164. Figs 7–9, Paralectotype (ZF 3973); spiral, umbilical and oblique-umbilical views, × 168.
All from *Challenger* station 346, South Atlantic.

Brady, which is thought worthy of formal description. This is given the name *Trochammina pintoi* sp. nov. and is described from *Challenger* station 323, at 1,900 fathoms (3,480 m), in the S.W. Atlantic (B.M.N.H. slide no. 1958.3.13.801–808). It is illustrated in Figs 10–14, 17.

Systematics

The material illustrated in this paper is housed in the collections of the Protozoa Section, Department of Palaeontology, registration numbers ZF 3971-ZF 3984 inclusive.

Family: **TROCHAMMINIDAE** Schwager, 1877
Subfamily: **TROCHAMMININAE** Schwager, 1877

Genus: ***TROCHAMMINA*** Parker & Jones, 1859
Type species: ***Nautilus inflatus*** Montagu, 1808.

Trochammina nana (Brady)

1881 *Haplophragmium nanum* Brady: 50.
1884 *Haplophragmium nanum* Brady; Brady: 311 (*pars*), pl. 35, figs 7, 8 only.
1960 *Trochammina nana* (Brady) Barker: 72 (*pars*), pl. 35, figs 7, 8 only [after Brady, 1884].

MATERIAL. 6 syntypes, B.M.N.H. slide no. ZF 1547, plus 2 further specimens from the type locality in the Heron-Allen & Earland Collection, ex Sidebottom '*Challenger* type-slide Collection', C12, square 6.

LECTOTYPE. B.M.N.H. ZF 3971, ex slide no. ZF 1547, *Challenger* station 346, north of Ascension Island, South Atlantic, lat. 2°42'S, long. 14°41'W, depth 2,350 fathoms (4,300 m). Believed to be the specimen figured by Brady, 1884, pl. 35, fig. 8. Refigured in Figs 1–3, 6, by scanning electron microscopy.

DESCRIPTION (LECTOTYPE). Test a loosely coiled trochospire, subcircular in umbilical and spiral views and strongly lobulate. In edge view, convex spirally, concave umbilically, well rounded at the periphery. Proloculus very large, followed by 9 subglobular chambers arranged in almost two whorls and increasing only slowly in size; 6 chambers in final whorl. Radial sutures deeply incised, straight to slightly curved. Umbilicus deep and open. Aperture an interiomarginal extra-umbilical arch with lip, without direct communication to the umbilical depression; because of loose coiling, apertures of the penultimate and antepenultimate chambers incompletely covered by the subsequent chambers and partially open. Wall agglutinated, single layered, imperforate and thin (5 µm). Agglutinant, very fine, consisting of quartz flakes and spicules of siliceous sponges. Colour light yellow-brown, except for the colourless final chamber.

DIMENSIONS (LECTOTYPE). Maximum diameter 410 µm, minimum diameter 340 µm, maximum width 200 µm. Maximum external proloculus diameter 120 µm. Diameter of umbilical depression 100 µm. Length of apertural opening 70 µm.

VARIATION (PARALECTOTYPES). The 5 paralectotypes from slide ZF 1547 are morphologically similar to the lectotype. The megalospheric specimen illustrated in Figs 7–9 (ZF 3973) is smaller with a test diameter of between 230 and 290 µm. The single microspheric individual (unfigured) has 17 chambers arranged in just over 2 whorls with 8 chambers in the final whorl; the test diameter ranges between 320 and 440 µm and the proloculus is 20 µm across at its widest point. Specimen ZF 3972 (Figs 4, 5) has a test diameter of between 240 and 290 µm and a large megalospheric proloculus of 90 µm maximum diameter. A fragment of a further paralectotype, placed in dilute HCl did not break down but turned colourless; the test is very slightly calcareous.

The '*Challenger* type-slide Collection' was originated by H. Sidebottom to illustrate examples of the species figured by Brady (1884) and was picked from topotypic material.

Sidebottom's specimens of *Trochammina nana* comprise a microspheric individual with a maximum diameter of 470 μm and 9 chambers in the last whorl and a megalospheric individual almost identical in size and morphology to the lectotype.

REMARKS. As all the specimens of *T. nana s.s.* examined exhibit the same overall test morphology, it is difficult to see why Brady thought them to represent aberrant specimens. In fact they seem to form a well defined taxon without close relatives within *Trochammina*.

The other specimen figured by Brady (1884, pl. 35, fig. 7) is dextrally coiled and cannot be recognized amongst the remaining syntypes nor in Sidebottom's *Challenger* type-slide.

DISTRIBUTION. Known only from the type locality. Recent.

Trochammina pintoi sp. nov.
Figs 10–14, 17.

?1881 *Haplophragmium nanum* Brady: 50 (?*pars*).
1884 *Haplophragmium nanum* Brady; Brady: 311 (*pars*), not illustrated.

DIAGNOSIS. A tightly coiled, 6–7 chambered, moderately inflated *Trochammina*, with a flat spiral side and broadly rounded at the periphery.

NAME. In honour of Dr Jrajá Damiani Pinto, of Porto Alegre, Brazil, for his contribution to the study of the microfauna, in particularly the Ostracoda, of the Brazilian Shelf.

MATERIAL. 8 specimens, B.M.N.H. slide no. 1958.3.13.801–808 plus 3 further specimens from the type-locality in the Heron-Allen & Earland 'Students' Collection'.

HOLOTYPE. B.M.N.H. ZF 3974, ex slide no. 1958.3.13.801–808, *Challenger* station 323, S.W. Atlantic (Argentine Basin), lat. 35°39′S, long. 50°47′W, depth 1,900 fathoms (3,480 m). Figured by scanning electron microscopy in Figs 12, 14, 17.

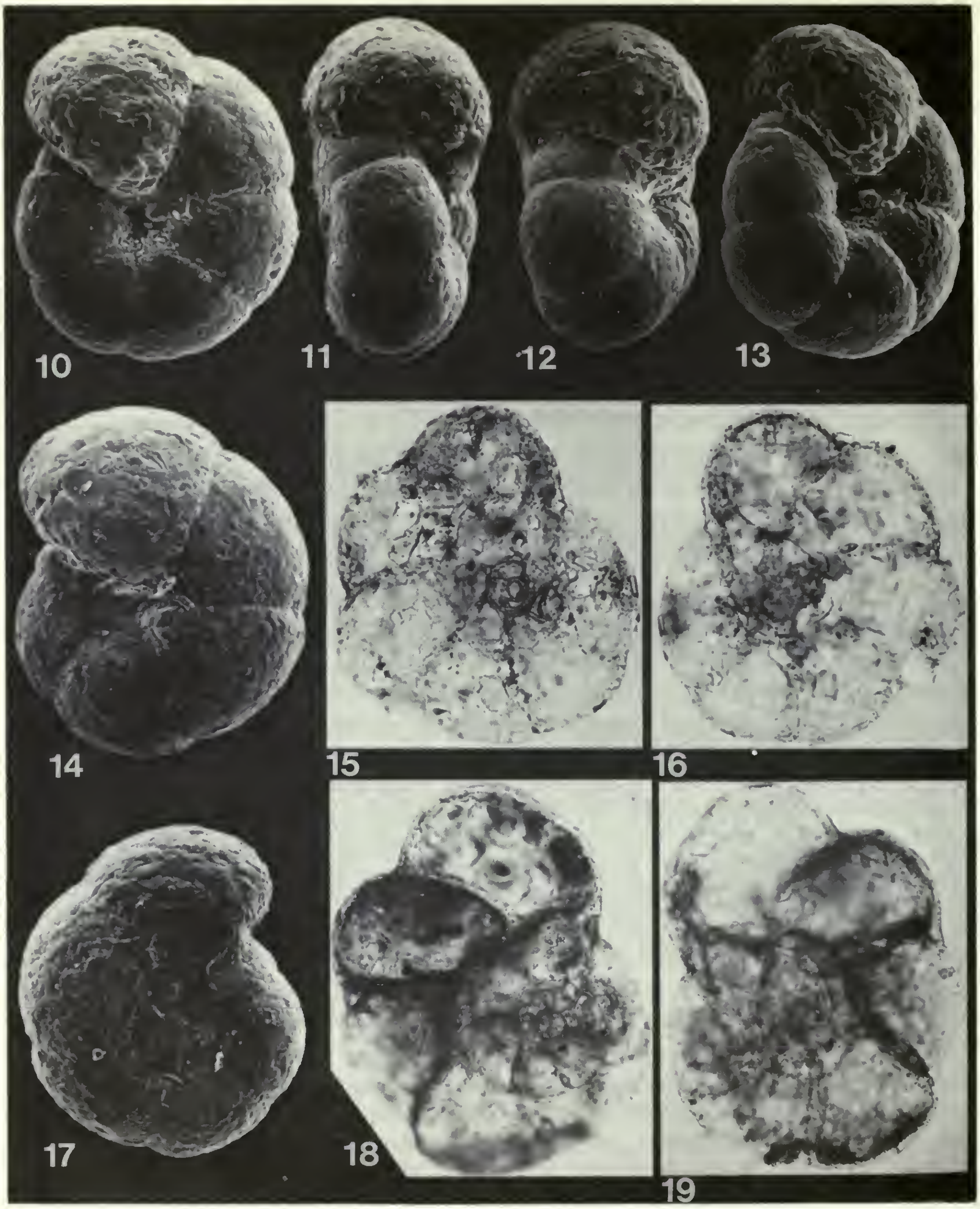
DESCRIPTION (HOLOTYPE). Test a trochospire of just over two whorls, moderately inflated but tightly coiled. Subcircular and virtually non-lobulate in umbilical and spiral views. In edge view, spirally flat, umbilically convex, broadly rounded at the periphery. Chambers inflated, closely embracing, 6 in final whorl, increasing only slowly in height and width; seen umbilically and spirally chambers sub-triangular in shape. On spiral side, early whorls form a slightly sunken area due to the overlap along the spiral suture of the chambers in the final whorl. Radial sutures straight, flush on spiral side, slightly depressed on umbilical side. Umbilicus tight. Aperture, a narrow umbilical peripheral slit without a lip, apparently separated from the umbilical depression and thus of *Trochammina*-type. Wall rather thick, agglutinated, single layered and imperforate, made up of quartz grains. Colour uniformly light brown-yellow.

DIMENSIONS (HOLOTYPE). Maximum diameter 350 μm, minimum diameter 310 μm, maximum width 220 μm.

VARIATION (PARATYPES). All the paratypes have a morphology very close to that of the holotype. The paratype (ZF 3975) illustrated in Figs 10, 11, 13, has 7 chambers in the final whorl, and about 21 chambers, including the proloculus, in all (the exact number of chambers and whorls cannot be determined). The maximum and minimum diameter of the test is 350 and 300 μm respectively, the greatest width 200 μm. The maximum diameter of the remaining paratypes ranges from 300 to 450 μm.

REMARKS. *Trochammina rossensis* Warthin from the Ross Sea, Antarctica (Warthin, 1934: 3, text-figs 1–3), shows similarities to our new species. In edge view, although the spiral side is also very flat the periphery of Warthin's species is sub-acute; moreover, it has the well developed umbilical flaps and aperture-type of a *Portatrochammina* (see below).

We have included, somewhat tentatively, the original reference to *H. nanum* (i.e. Brady, 1881) at least in part, in our synonymy of *T. pintoi*. This is because our new species comes from a South Atlantic *Challenger* station, as does the true *T. nana*, even though the



Figs 10–14, 17 *Trochammina pintoi* Brönnimann & Whittaker sp. nov. Figs 12, 14, 17, Holotype (ZF 3974); edge, umbilical and spiral views: figs 12, 17, × 132; fig. 14, × 135. Figs 10, 11, 13, Paratype (ZF 3975); umbilical, edge and oblique-umbilical views, × 132.
Both from *Challenger* station 323, S. Atlantic.

Figs 15, 16, 18, 19 *Portatrochammina bipolaris* Brönnimann & Whittaker sp. nov. Figs 15, 16, Paratype (ZF 3976); spiral and umbilical views in immersion oil, × 178. Figs 18, 19, Paratype (ZF 3977); spiral and umbilical views in immersion oil, × 200.
Both from the Beaufort Sea (N.W. Canada), Arctic Ocean.

type-description of the latter does not seem to allow for its morphology, nor is it illustrated by Brady in any of his subsequent papers. It is more likely, however, that only later, in collating the data for his *Challenger* Report (1884), did Brady decide to include this form (the type-locality of *T. pintoi* is listed under the distribution of *H. nanum*: Brady, 1884, p. 312) within his wide concept of that taxon.

DISTRIBUTION. Known only from the type-locality. Recent.

Genus: ***PORTATROCHAMMINA*** Echols, 1971

Type species. ***Portatrochammina eltaninae*** Echols, 1971

Portatrochammina bipolaris sp. nov.

Figs 15, 16, 18, 19–31.

1881*a* *Haplophragmium nanum* Brady; Brady: 406, pl. 21, figs 1a–c (*non H. nanum* Brady, 1881).
1882 *Haplophragmium nanum* Brady; Brady: 99, pl. 2, figs 1a–c.
1884 *Haplophragmium nanum* Brady; Brady: 311 (*pars*), pl. 35, figs 6a–c only.
1894 *Haplophragmium nanum* Brady; Goës: 22 (*pars*), pl. 5, figs 124–126 only.
1920 *Trochammina nana* (Brady) Cushman: 7, pl. 1, fig. 4.
1920*a* *Trochammina nana* (Brady); Cushman: 80, pl. 17, fig. 1 [after Brady, 1884, pl. 35, figs 6a–c].
?1931 *Trochammina nana* (Brady); Wiesner: 112, pl. 17, fig. 202.
?1948 *Trochammina nana* (Brady); Cushman: 42, pl. 5, figs 1a–c.
1952 *Trochammina nana* (Brady); Phleger: 86, pl. 13, figs 31, 32.
1953 *Trochammina nana* (Brady); Loeblich & Tappan: 50, pl. 8, fig. 5.
1960 *Trochammina nana* (Brady); Jarke: 619, pl. 4, figs 10a, b.
1960 *Trochammina nana* (Brady); Barker: 72 (*pars*), pl. 35, figs 6a–c only [after Brady, 1884].
1969 *Trochammina nana* (Brady); Vilks: 45, pl. 1, figs 23a, b.
1971 *Portatrochammina wiesneri* (Parr); Echols: 166 (*pars*), pl. 7, figs 2a–c (?1a–c) only (*non Trochammina wiesneri* Parr, 1950).

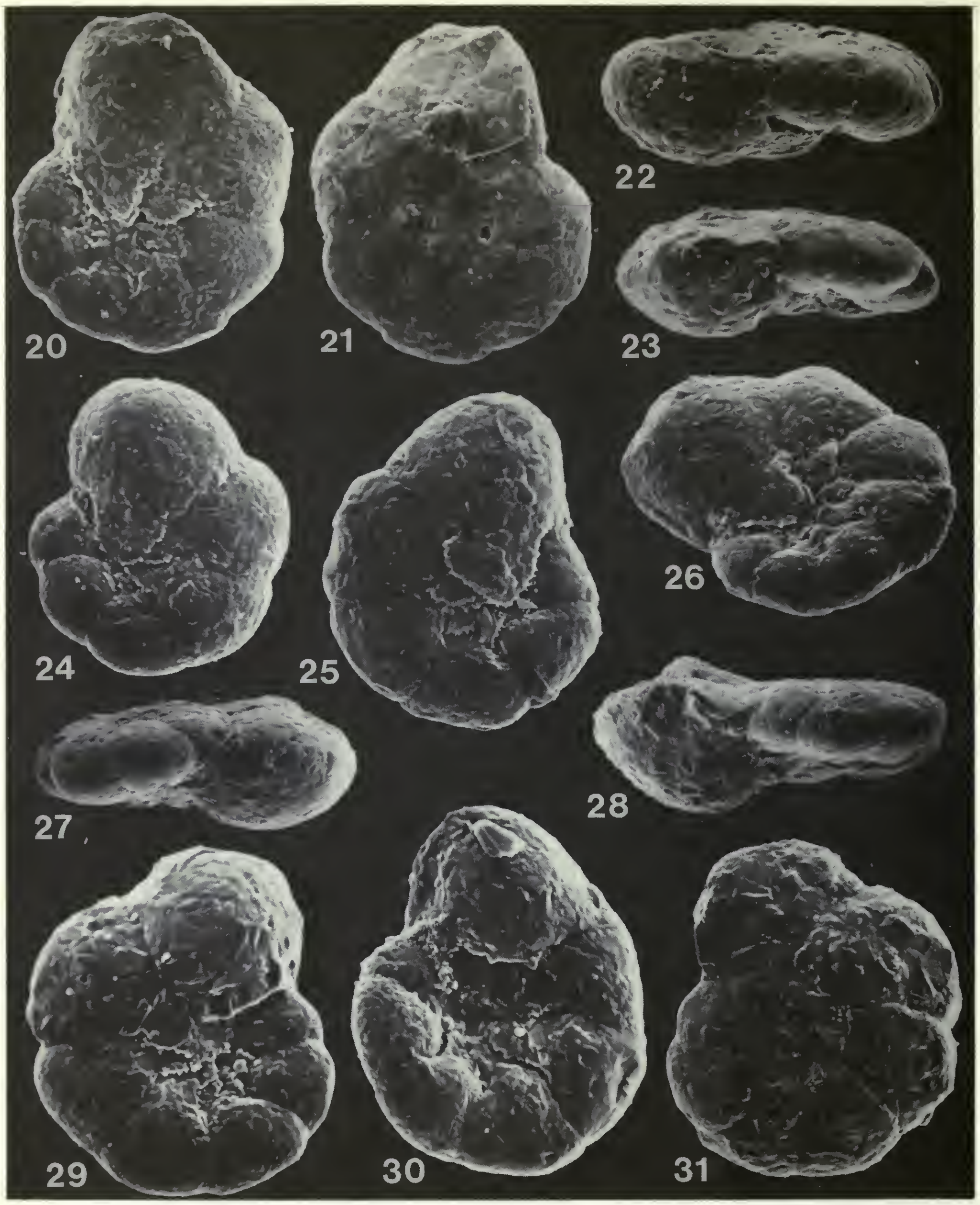
DIAGNOSIS. A small compressed *Portatrochammina* with 6–8 chambers in the final whorl. Edge view with diagnostic flat or only slightly convex spiral side. Last formed chambers increasing rapidly in size and quite lobulate. Umbilical area wide but shallow and covered by a series of well developed overlapping flaps.

NAME. Alludes to the bi-Polar distribution of this species.

MATERIAL. Over one hundred specimens from various Austro–Hungarian North Polar Expedition stations to the south of Franz-Josef Land, and about 40 specimens from the vicinity of the South Shetlands and Graham Land, Antarctica (material from *Discovery* and *Terra Nova* Expeditions), both in the Museum Collections; several specimens from the Beaufort Sea, N.W. Canada, donated by Drs Schafer & Vilks.

HOLOTYPE. B.M.N.H. ZF 3979, selected from about 40 specimens in slide no. ZF 1546, Austro–Hungarian North Polar Expedition station 518, off Franz-Josef Land, Arctic Ocean, depth 113 fathoms (207 m). The slide is labelled as containing specimen(s) figured by Brady, 1881a, pl. 21, figs 1a–c and Brady 1884, p. 35, figs 6a–c, but actual specimen(s) cannot be recognized. Figured by scanning electron microscopy in Figs 20, 21, 26.

DESCRIPTION (HOLOTYPE). Test a low trochospire; elongate-ovate in outline in umbilical and spiral views, final portion somewhat lobulate. In edge-view, compressed, almost flat spirally, concave umbilically and rounded to sub-acute peripherally; final chamber characteristically flat on the spiral side and strongly convex on the umbilical side. Chambers about 14 in number, radially elongate and tangentially short; 7 in the final whorl, overlapping at the umbilical ends along the radial sutures; later formed chambers increasing rapidly in size. Radial sutures straight to sinuous on the umbilical side and slightly curved on the spiral side. Shallow umbilical depression covered by the partially overlapping free umbilical flaps of the chambers of the final whorl, typical of a *Portatrochammina.* Aperture begins as a low interiomarginal opening near the periphery extending as a slit around the umbilical flap; last



Figs 20–31 *Portatrochammina bipolaris* Brönnimann & Whittaker sp. nov. Figs 20, 21, 26, Holotype (ZF 3979); umbilical, spiral and oblique-umbilical views, ×176. Figs 22, 25, Paratype (ZF 3980); edge and umbilical views, × 200. Figs 23, 29, 31, Paratype (ZF 3981); edge, umbilical and spiral views: fig. 23, × 172; figs 19, 21 × 180. Figs 24, 27, Paratype (ZF 3982); umbilical and edge views, × 168 and × 182 respectively. Fig. 28, Paratype (ZF 3983); edge view, × 152. Fig. 30, Paratype (ZF 3984); oblique-umbilical view, × 250.

Figs 20, 21, 24, 26, 27, from Austro–Hungarian North Polar Expedition, station 518, off Franz-Josef Land (U.S.S.R.), Arctic Ocean (between lats. 79° and 80°N). Fig. 28, from Austro–Hungarian North Polar Expedition, station 516, off Franz-Josef Land, depth 130 fathoms (238 m), ex Brit. Mus. Nat. Hist. slide no. 1955.10.1.312–345. Figs 22, 25, from *Discovery* station 177, off South Shetland Islands, Antarctica (lat. 63°18′S, long. 60°20′W), depth 1,080 m, ex Heron-Allen & Earland 'type-slide' no. 697, square 54. Figs 23, 29–31, from the Beaufort Sea (N.W. Canada) Arctic Ocean (north of lat. 70°N).

formed aperture, as well as preceeding apertures being in direct communication with the umbilical depression and presumably all functional. Wall agglutinated, single layed and imperforate, consisting of very fine quartz elements interspersed locally with irregular shaped, larger grains. Colour of early portion of test dark brown, grading into lighter brown, final chamber virtually colourless.

DIMENSIONS (HOLOTYPE). Maximum diameter 270 µm, minimum diameter 200 µm, width 70 µm. Proloculus diameter 10 µm.

VARIATION (PARATYPE). Figs 22–25, 27–31, show both six and seven chambered forms and illustrates the variation in morphology in spiral, umbilical and edge views. Particularly variable is the chamber shape and lobulation of the final portion of the test and the length of the free portion of the umbilical flap of the last-formed chamber; in some forms this flap can almost cover the earlier flaps (e.g. Fig. 24), in others it is short, so that the flaps of all the chambers in the final whorl are exposed (e.g. Fig. 29). The maximum diameter of the specimens examined in our study varied between 150 and 320 µm. The number of whorls varies between about 2½ and 3.

Two specimens donated by Drs Schafer & Vilks (ZF 3976, ZF 3977) are illustrated in a clearing medium (Figs 15, 16, 18, 19). The proloculus can be clearly seen and in both cases has a diameter of about 20 µm. The wall of the final chamber is 2–3 µm thick. In dilute HCl, the tests do not disintegrate nor does the colour change; the wall is very slightly calcareous.

REMARKS. Unambiguous references to our new species, with good illustrations, are not common in the literature. In particular, no mention is made of the umbilical flaps in earlier papers nor can they be readily seen in many published figures; the most surprising example of this omission being Brady himself (1881*a*; 1884), whereas we know, from the type-material that the flaps exist. The vast majority of citations of *Haplophragmium nanum* or *Trochammina nana auctt.*, nevertheless, do not belong to any of the three species revised in this paper.

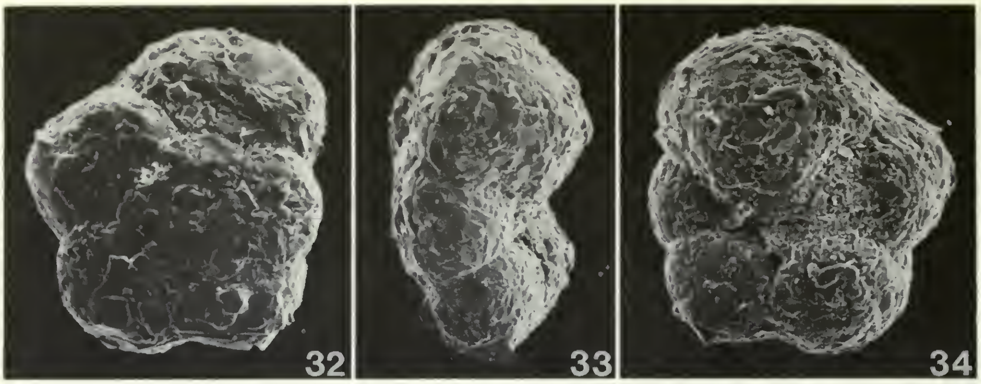
That the species should occur in both Polar seas and not elsewhere, is perhaps surprising, but the Antarctic form (see Figs 22, 25) would appear identical to that from the Arctic (Figs 20, 21, 23, 24, 26–31). The Antarctic specimens of *P. bipolaris* have been checked against the types of the species of Trochamminidae described by Parr (1950), and preserved in the South Australian Museum, Adelaide, and those of Heron-Allen & Earland (1922; 1932) and Earland (1933–36) in this institute, all from that region. None would appear to be synonymous with our new species.

A specimen of the type-species of *Portatrochammina, P. eltaninae* Echols, from the *Terra Nova* Expedition, station 194 (26), collected off Oates Land, Antarctica (lat. 69°43′S, long. 163°24′E), is illustrated in Figs 32–34, for comparison with *P. bipolaris.* It has been checked against the holotype of Echol's species (U.S. National Museum reg. no. 687210; figured in Echols, 1971, pl. 8, figs 1a–d). *P. eltaninae* is a five-chambered species and is less compressed and has more globose chambers than *P. bipolaris*; furthermore, the umbilical flap of the last-formed chamber almost completely covers the umbilicus.

DISTRIBUTION. Arctic Ocean – widespread in the Canadian Arctic (Cushman, 1920; Phleger, 1952; Vilks, 1969; Schafer & Vilks's material, herein); around Greenland (Phleger, 1952; Loeblich & Tappan, 1953); the Russian (Brady, 1881*a*; 1882; Jarke, 1960, and material herein) and Scandinavian Arctic (Goës, 1894; Jarke, 1960). Its most southerly substantiated record in the N. Hemisphere is from the Faroes Channel (slide marked 'cold area', *Porcupine* Expedition material, B.M.N.H.).

Antarctic – Scotia Sea (as *P. wiesneri* (Parr); Echols, 1971); off the South Shetlands and Graham Land (Heron-Allen & Earland, 1922; 1932, unfigured, but verified from their collections, see herein).

A Recent species only, as far as we are aware. Records exist back to the Cretaceous (e.g. Chapman, 1892: 6, pl. 5, figs 15a–c), but these are not conspecific. A shelf species, living down to about 1,000 m, but in Arctic waters commonly found between 150 and 300 m.



Figs 32–34 *Portatrochammina eltaninae* Echols. ZF 3978. Spiral, edge and umbilical views of same specimen, for comparison with *P. bipolaris*, × 142.
From British Antarctic (*Terra Nova*) Expedition station 194 (26), off Oates Land, Antarctica, depth 180–200 fathoms (329–366 m) ex Heron-Allen & Earland 'type slide' no. 316, square 16.

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Crinoidea collected by the *Meteor* and *Discovery* in the NE Atlantic

A. M. Clark
Department of Zoology, British Museum (Natural History), Cromwell Rd., London SW7 5BD

Introduction

The paper includes new records for mostly little-known Crinoidea collected by the *Meteor* and *Discovery* in the Atlantic from off NW Spain to the vicinity of the Canary Islands and from the Great Meteor Bank, S from the Azores, the source of a new genus and species, *Meteorometra monticola*. Tables of numerical data for some of the less well-known species are provided. The ranges of several species are extended and affinities of some discussed. A distribution map is included.

Systematic descriptions

Family COMASTERIDAE

Neocomatella europaea A. H. Clark

Actinometra pulchella (part) P. H. Carpenter, 1888: 304–306, pl. 4, pl. 52, fig. 1; Koehler & Vaney, 1910: 32. [Non *A. pulchella* Pourtalès, 1878.]

Neocomatella europaea A. H. Clark, 1913*a* : 4; 1931 : 150–153; Cherbonnier, 1970*a* : 343, 345, 346, 347; 1970*b* : 1266, 1268, 1269, 1270, 1271; Sibuet, 1974 : 791.

MATERIAL. *Meteor* cruise 9c, st. 101b AT 33, 36°36·3′N, 14°14′W (Josephine Bank, W of Portugal); 170–300 metres; 5 specimens.

Discovery st. 8966, 31°21–22′N, 10°40·5–39·2′W (off Morocco); 686–742 metres; 1 specimen.

Discovery st. 9015, 28°46·8–46·0′N, 12°47·4–46·8′W (off S Morocco); 610–637 metres; arms only.

The description of this species given by A. H. Clark is limited mainly to the form of the cirri. Unfortunately all the present specimens are badly broken but some descriptive remarks can be made from them.

All probably had c. 20 arms, not exceeding 40–50 mm in length. One of the larger *Meteor* specimens and the *Discovery* one both have the arm breadth at the first syzygy (which is usually 1 + 2) 1·1 mm. The strong, incurled cirri are one or two deep around the discoidal centrodorsal, numbering only XVIII plus ii immature ones in one specimen but XXXIII in another. There are up to 15 cirrals, laterally compressed, the distal ones broadened dorsoventrally. The longest segment, the fourth or fifth, measures up to 1·3 mm, with length : median breadth 3·2–3·5 : 1; the total cirrus length being up to 12 mm. There are small dorsal spines on the distal segments.

The division series are rounded laterally. The ossicles are not at all flared at the joints but are ornamented along their distal edges by a series of very fine rugosities. All the IIBr series are of two ossicles. On the brachials the ornamentation becomes stronger, the outer part is fluted, each small ridge leading to a distally-directed spine, though the ossicle is slightly

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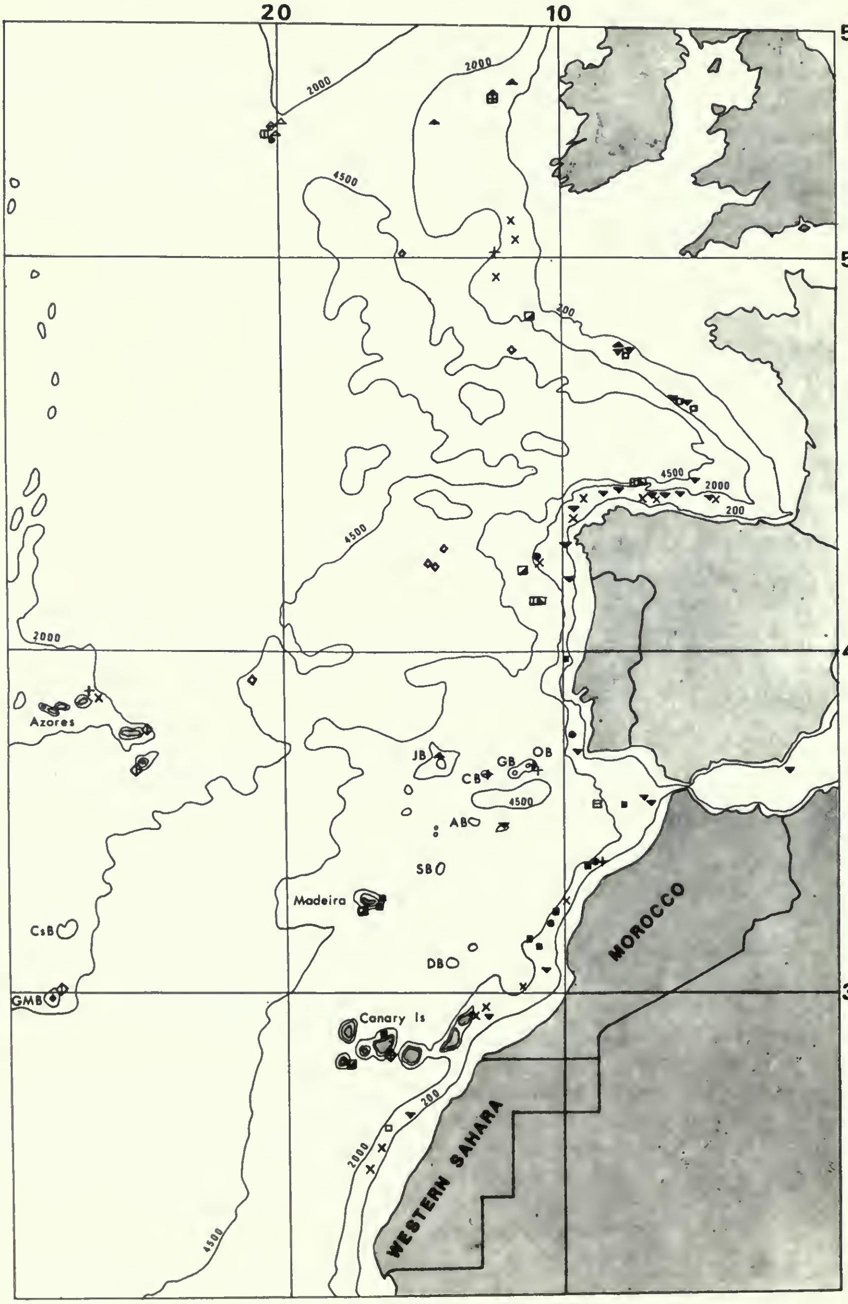
flared and the profile is irregular. Combs are present on the first three pinnules, which on one specimen have c. 30, c. 25 and c. 24 segments respectively, P_1 measures 7·0 mm.

Distribution. Northern Bay of Biscay to Western Sahara, NW Africa; 337–1700 metres.

Affinities. Messing (MSc thesis, 1975) has studied a large collection of *Neocomatella pulchella* (Pourtalès) from the West Indian area, ranging to St. Paul's Rocks, NE from Brazil. He noted that a relatively small specimen with arm length only c. 50 mm (compared with the usual 100+ length of most examples of this species collected) has XVI cirri, with 14–17 segments, measuring 10 mm in length, not markedly different from the specimens of *N.*


20
10
55
50
40
30
2000
4500
200
Azores
Madeira
Canary Is
JB
GB
OB
CB
AB
SB
DB
CsB
GMB
MOROCCO
WESTERN SAHARA

europaea mentioned above. However, already at this size, the longest cirrals in the West Indian specimen have length : median breadth only 2.1 : 1 and the cirri must be much stouter, otherwise it might be thought that the eastern Atlantic *Neocomatella* is only a stunted paedomorphic form of the West Indian species.

Family THALASSOMETRIDAE

Koehlermetra porrecta (P. H. Carpenter)

Antedon porrecta P. H. Carpenter, 1888 : 250–252, pl. 52, figs 3–5; Koehler & Vaney, 1910 : 32; Hartlaub, 1912 : 285.
Antedon flava Koehler, 1895: 475; Koehler & Vaney, 1910 : 31.
Crotalometra porrecta: A. H. Clark, 1913*b* : 46; Mortensen, 1927 : 25.
Koehlermetra porrecta: A. H. Clark, 1950 : 101–105.
Koehlermetra flava: A. H. Clark, 1950 : 105–107.

MATERIAL. *Meteor* cruise 36, st. 98 AT 149, 25°31·5′N, 16°02·2′W (off Western Sahara); 658–888 metres; 12 specimens.
Discovery st. 7984, 25°27′N, 16°10′W; 811–890 metres; 2 adult specimens and 1 pentacrinoid.

All the specimens are somewhat broken, often from the first syzygy, which is at 2 + 3 on arms following IIBr series of four ossicles – the usual number, or at 3 + 4 on arms based on IIBr series of two, occasionally at 1 + 2 or even not until 10 + 11. Where more than one IIBr series occur, these are usually adjacent and posterior.

The centrodorsal is domed in one specimen, otherwise more or less broadly truncated, even to the extent of being discoidal. Measurements are given in table 1. The cirri are arranged one or two deep around the sides. The sixth or seventh cirral is usually a transition segment and is the longest; it has a triangular raised patch dorsally.

The division series are quite smooth except sometimes for a few small knobs at the sides. They have a flattened shoulder-like flange each side continuing distally into the base of the first pinnule (P_D) on the IIBr_2.

The larger specimens have c. 20 arms. The arm length in one of them (the third in table 1, taken by the *Discovery*) was probably 120–130 mm. This specimen has c. 12 segments in

Fig. 1 Map of part of the NE Atlantic, with contours for 200, 2000 and 4500 metres, showing records of the following 18 species of bathyal and abyssal Crinoidea:

▼ *Neocomatella europaea* A. H. Clark
■ *Thalassometra lusitanica* (P.H.C.)
◆ *Meteorometra monticola* n.sp.
● *Trichometra cubensis* (Pourtalès)
× *Pentametrocrinus atlanticus* (Perrier)
◇ *Bathycrinus gracilis* Wyville Thomson
⊟ *Rhizocrinus magnus* Gislén
◫ *Zeuctocrinus gisleni* A. M. Clark
◪ *Gephyrocrinus grimaldii* Koehler & Bather
□ *Koehlermetra porrecta* (P. H. Carpenter)
◈ *T. omissa* (Koehler)
▲ *Orthometra hibernica* (A.H.C.)
⊞ *Atelecrinus balanoides* P.H.C.
△ *Thaumatocrinus jungerseni* A.H.C.
+ *Democrinus parfaiti* Perrier
◩ *Porphyrocrinus thalassae* Roux
⬙ *Anachalypsicrinus nefertiti* A.M.C.
◇ *Cyathidium foresti* Cherbonnier & Guille

(*Note:* A few of the older records, e.g. from *Porcupine* and *Travailleur* have been slightly modified to conform with the depth contours.) An additional seven stalked species have been recorded from the area, namely: *Annacrinus wyvillethomsoni* (Jeffreys *in* W. Thomson) (from the Bay of Biscay to the Canary Is in 1330–2000 metres); *Porphyrocrinus incrassatus* Gislén (Bay of Biscay, also St. Helena, 2400–2780 metres); *Conocrinus cabiochi* Roux (Bay of Biscay, 1975–2070 metres); *C. cherbonnieri* Roux (Bay of Biscay, 330–510 metres); *Monachocrinus perrieri* (Koehler & Vaney) (off Morocco and the Azores, also South Africa, 1620–4600 metres); *M. recuperatus* (Perrier) (off Morocco and Azores, 2300–4260 metres); also ?*Democrinus conifer* (A. H. Clark) but the Josephine Bank and Portuguese records of A. H. Clark (1923) at least are probably conspecific with *D. parfaiti*, as already noted (A. M. Clark, 1977 : 177). The abbreviations for the sea mounts are as follows: AB – Ampere Bank; CB Cromer Bank; CsB Cruiser Bank; DB Dacia Bank; GB Gettysburg Bank; GMB Great Meteor Bank; JB Josephine Bank; OB Ormonde Bank; SB Seine Bank. (Gettysburg and Ormonde Banks together make up the Gorringe Ridge).

Table 1 *Koehlermetra porrecta* (P. H. Carpenter). Numerical data from 11 *Meteor* and 2 *Discovery* specimens. The length to the first brachial syzygy at Br2 + 3 includes a IIBr4 series; the relative length of the transition segment of the cirri uses the median width; immature cirri are counted in small roman numbers.

Arms		Centrodorsal		Cirri			Trans. seg.		P_D		P_I	
Width at 2 + 3	Length to Br2 + 3	Diam.	Height	No.	Segs.	L.	No.	L/W	Segs.	L.	Segs.	L.
2·7	10·2	7·5	2·3	XXII + iv	33–35	38	7	1·7	—	—	—	—
2·4	9·7	7·2	2·6	XXIV	39	45	8	1·9	—	—	—	—
2·5	10·0	7·0	2·5	XX + vi	39	40	7	1·4	20	c. 12·5	16–18	12
2·6	10·5	6·2	2·5	XXI + iv	—	—	—	—	21	13·4	17+	c. 12
2·5	9·5	6·7	3·0	XXIV	—	—	—	—	21+	c. 13·5	—	—
2·7	9·3	6·7	2·5	XIV + vi	—	—	—	—	—	—	19	9·3
2·2	c. 9·5	6·0	2·1	XVIII	32, 36	29	7	1·9	17, 19	10·0	15	c. 9·5
2·2	9·0	5·9	2·0	XXI	37	39	7	1·5	17	10·5	—	—
2·0	8·5	5·6	2·0	XXII	34	29	6	1·6	—	—	—	—
2·0	9·2	4·6	2·2	XVIII	28	23	6	1·9	18	c. 9·2	17	c. 9·0
2·0	8·5	4·7	1·9	XXIII	31–34	26	6	2·0	15	7·9	14	7·3
		2·8	1·75	XIX	27, 29	17·5	6	1·6	—	—	—	—
				XV + v	25	c. 17	5		14	5·2	11	3·7

P_2, which measures c. 7·5 mm; there are 18 segments in P_3, total length 12 mm; P_4 is similar to P_3. The smaller *Discovery* specimen has only 11 arms, c. 40 mm long. On the only pair of arms following the single IIBr series, its P_2 has 8 segments and is 2·6 mm long.

The pentacrinoid has 10 arms c. 15 mm long. The longer cirri have 15, in one case 16, segments, the fourth of which is a transition segment. The dorsal projections have sharper points than in the larger specimens. The division series are already flanged laterally but the edges of the flanges are not as straight as in the larger specimens. About 10 segments of the stalk remain, the distalmost much shorter than the proximal ones. There is a small P_1 of c. 6 segments, then a gap until P_5.

SYNONYMY. A. H. Clark (1950) distinguished two species of his new genus *Koehlermetra,* the type-species, *Antedon porrecta,* type locality near Ascension Island, S Atlantic, but subsequently recorded from the Bay of Biscay, and *A. flava* Koehler, type locality in the Bay of Biscay. In his key he separated them on the number of the cirrus segments, cited as 40–50 in *K. porrecta* (cirrus length c. 55 mm) and c. 30 in *K. flava* (cirrus length not given but noted by Hartlaub (1912) as 35–38 mm). No estimate of arm length was given for the holotype of *K. flava,* but that of *K. porrecta* was put at c. 150 mm.

The three syntypes of *K. porrecta* are in the British Museum collections. The largest has the centrodorsal diameter as much as 8 mm and the length from IBr_1 to Br_{2+3} (including a IIBr series of four ossicles) is 11·7 mm. However, the arm breadth at 2 + 3 is 2·6 mm, as in the largest *Meteor* specimens. It has only two peripheral cirri left intact; both have 49 segments and measure 51 or 52 mm. Another syntype has centrodorsal diameter 6·0 mm; all the arms are broken at the first syzygy (i.e. $IIBr_3$ or Br_3); its only intact cirrus is an immature one and has 42 segments. The third and smallest syntype with centrodorsal diameter 3·9 mm has peripheral cirri with 31 and 32 cirrals and measures c. 23 mm in length. The same measurements and counts for a comparable *Meteor* specimen are 4·6 mm, 28 cirrals and cirrus length 23 mm. The *Meteor* and *Discovery* specimens are clearly intermediate between the descriptions of *K. porrecta* and *K. flava* and show enough variation to support Hartlaub's suggestion (1912) that the two are conspecific. It is rather extraordinary that Koehler & Vaney (1910) recorded both *Antedon porrecta* from the Bay of Biscay and *A. flava* from the vicinity of the Canary Islands, without comment.

Thalassometra lusitanica (P. H. Carpenter) new comb.

Antedon lusitanica P. H. Carpenter, 1884*a* : 368; 1888 : 109–110, pl. 39, figs 1–3; 1891 : 65–67.
Antedon (Crotalometra) lusitanica: Koehler & Vaney, 1910 : 31.
Thalassometra lusitanica: A. H. Clark, 1911*a* : 37.
Stiremetra lusitanica: A. H. Clark, 1923 : 40; Mortensen, 1927 : 25; A. H. Clark, 1950 : 121–126.
? Thalassometrid. Gislén, 1955: 84.

MATERIAL. *Meteor* cruise 8, st. 19 AT 9, 33°34·2′N, 09°19·3′W (off Morocco); 1300 metres; 1 specimen.

Meteor cruise 23, st. 174 AT, 35°30·6′N, 08°07·3′W–35°37·5′N, 08°03·2′W; 1716–1912 metres; 5 specimens.

Discovery st. 8967, 31°25·9′N, 10°53·7′W–31°26·3′N, 10°50·8′W (off Morocco); 1140–1222 metres; 28 specimens.

Discovery st. 9028, 31°26·1–28·1′N, 10°52·8–50·3′W (off Morocco); 1229–1166 metres; 17 specimens.

Some numerical details of ten of the specimens from *Discovery* station 8967 are given in table 2.

The maximum arm number in the *Discovery* specimens is 16, possibly 17, but 12–14 is more usual. Only one of the six *Meteor* specimens definitely has more than ten arms, the single IIBr series being of four ossicles. Some *Discovery* specimens have IIBr2 series but more often IIBr4, as on three adjacent radii of the one with a total of 16. Breakage of the division series and arms is frequent, rarely more than half the likely arm length remaining; the maximum was probably c. 60 mm.

Table 2 *Thalassometra lusitanica* (P. H. Carpenter). Numerical data from 10 specimens from *Discovery* st. 8967. The arm width is taken at the first syzygy after the first axillary, which is therefore either Br3 + 4 or IIBr3 + 4; length is to this same joint; the cirri often obscure the diameter of the centrodorsal; immature cirri are counted in roman numbers.

	Arms				Cirri									
	Width	Length	Centrodorsal					Trans.	P_1		P_2		P_3	
No.	at 3 + 4	to 3 + 4	Diam.	Height	No.	Segs	L	seg.	Segs	L	Segs	L	Segs	L
11(?13)	1·6	4·2	—	2·7	XV	58	40	5	14	4·2	—	—	—	—
14(?15)	1·5	4·2	—	2·5	XIV	56, 57	39	5–7	14	4·6	—	—	12	3·7
13(?15)	1·6	3·9	3·0	2·0	XVI + ii	—	—	—	16	5·0	—	—	—	—
16(?17)	1·6	3·8	—	2·3	XVII + ii	—	—	—	—	—	—	—	—	—
12(?14)	1·5	3·9	—	2·5	XIV	52, 53	35	5	17	5·0	11	3·0	11	3·3
10	1·4	4·0	2·75	2·25	XV	—	—	—	14	4·6	—	—	11	3·25
10?+	1·3	4·0	—	2·25	XV	54	37	5	15	4·6	12	3·2	—	—
13	1·3	3·9	2·9	2·1	XVII	54, 59	35	5	—	—	—	—	—	—
10?+	1·3	3·8	—	2·25	XVI	50	30	4, 5	16, 17	5·0	11	2·7	9	2·3
11(?12)	1·25	3·5	—	—	XVIII	50, 54	35	5(4)	—	—	—	—	—	—

The centrodorsals are rounded conical or hemispherical, always broader than high, diameter/height 1·2–1·5/1; the apical area is very papillose. There are X–XX cirri arranged in ten columns but the adapical ones are often reduced (obsolete in A. H. Clark's terminology) so that the functional number is nearer X. The columns are separated by a vertical ridge in each interradius and there may be a short radial ridge between the peripheral sockets only. The largest *Discovery* specimen (arm length ?c. 60 mm) has up to 59 cirrus segments; another with 50–54 cirrals in the peripheral cirri has 31 in an apical cirrus with a length of 15 mm as opposed to c. 35 mm. The maximum segment number in the *Meteor* specimens is 47. The fifth cirral is usually the transition segment, sometimes the fourth, or in apical cirri the third, rarely in large cirri the sixth or even seventh. Length/median width of the transition segment in larger specimens is 2·3–2·7/1.

The short, flared proximal cirrals, the straight-sided division series, the brachials and pinnules are all finely rugose or even spinose, more so in larger specimens. The more distal brachials remaining have a flared spinose distal median area but are rounded in section, not carinate.

The straight side of the division series continues as far as P_1, which is massive basally in contrast with P_2. The S-shaped curvature of P_1 makes estimate of its length difficult. All the pinnules are very prismatic.

The disc and ambulacra of the arms are coarsely and irregularly plated.

GENERIC POSITION. Contrary to the diagnosis of *Stiremetra lusitanica* given in A. H. Clark's monograph (1950) the cirri are not 'roughly in 15 columns' but in 10. Although one of the three syntypes in the British Museum collections has three cirri in each radius only two are peripheral, the third being in a column with one of them. Also many specimens, including one of the syntypes, and most of the *Meteor* and *Discovery* specimens have at least the proximal and distal edges of the division series and brachials distinctly rugose and sometimes there are also very fine spines on their surfaces, especially laterally. Accordingly these do not run down to *Stiremetra* in the 1950 key but to *Thalassometra*, of which there are two Atlantic species, *T. setosa* (A. H. Clark) from off Tristan da Cunha and *T. omissa* (Koehler) from the Canary Islands. The species of *Stiremetra* otherwise are all from outside the Atlantic and are said to have cirri in fifteen columns. Since young specimens are likely to go through a transitional stage with only ten columns and A. H. Clark has included in *Thalassometra* species with both ten and fifteen, this character does not seem to be of generic weight, though could be used specifically in comparisons of adult specimens.

Affinities. Both *Thalassometra setosa* and *T. omissa* are known only from single specimens. The holotype of *T. setosa* was re-examined. The arms are all badly broken; the width at Br3 + 4 is 1·1 mm and the length to this syzygy (including a IIBr series of 4) is 3·7 mm, only a little less than in the smaller specimens of *T. lusitanica* in table 2, from which it differs in having as many as XXX cirri in 15 columns but with up to only 35 cirrals; the division series are finely 'setose' all over and show no sign of the large synarthrial tubercle developed in *T. lusitanica.*

Judging from Koehler's description (1909), *T. omissa* has the cirri in only ten columns, contrary to A. H. Clark's interpretation, but the cirral number is given as only 21. The arms were all broken by 30 mm and if the total length was appreciably less than 50 mm and the cirrus counted was not a peripheral one the holotype might prove to be conspecific with *T. lusitanica.* The edges of the proximal brachials are described as finely spinose.

For further remarks on *Thalassometra omissa* see p. 197.

Gislén (1955) has recorded two arm fragments of a thalassometrid from off Las Palmas, Canary Islands at 670–1100 metres, with erect spinose ends to the ossicles (brachials and pinnulars). He thought them to be probably of *T. omissa* but the present observations on rugose ossicles in *T. lusitanica* make that a likely candidate.

Family **ANTEDONIDAE**

Antedon bifida (Pennant)

Asterias bifida Pennant, 1777 : 55.
Antedon bifida: Clark & Clark, 1967 : 179–226, fig. 13b, g, h; A. M. Clark, 1970: 28–30, figs 7, 8.

Material. *Meteor* cruise 9c, st. 90a AT 23; 37°22·8′N 09°00·7′W (off Portugal); 150–170 metres; 2 specimens.

Meteor cruise 9c, st. 90d AT 26; 37°21·5′N, 09°12·5′W; 320–385 metres; 1 specimen.

Meteor cruise 36, st. 122 KD 173, 33°17·2′N, 08°34·5′W (off Morocco); 65 metres; 1 specimen [? *A. bifida*].

In the Portuguese specimens the cirri are markedly deeper distally than proximally, as in *A. bifida moroccana,* which I think now should be ranked as no more than a form of *A. bifida.* This distal enlargement is much less marked in the Moroccan specimen, which is only provisionally referred to *A. bifida.*

Antedon sp. ? ***A. hupferi*** Hartlaub

[*Antedon hupferi* Hartlaub, 1890 : 171; Clark & Clark, 1967 : 153–157, fig. 13d.
Antedon dübeni (part): Gislén, 1955 : 86–87, pl. 1, fig. 4, pl. 2, fig. 8.]

Material. *Meteor* cruise 9c, st. AT 19, 31°35′N, 10°10·5′W (off Morocco); 150–160 metres; 1 specimen.

As noted in 1967, I disagree with Gislén (1955) that the *Antedon* with slender cirri from West Africa is conspecific with *A. duebeni* from the tropical west Atlantic. In this specimen all the peripheral cirri are broken; the most nearly complete one has 17½ segments with probably 1½ missing. The elongated shape of the segments and the fact that there are more than 17 (the maximum number given for *A. duebeni* by Gislén) agree better with *A. hupferi* in which up to 18 cirrals are recorded. If this identification is correct, the range of *A. hupferi* is extended northwards from Sierra Leone to Morocco.

Leptometra celtica (M'Andrew & Barrett)

Fig. 2

Comatula celtica M'Andrew & Barrett, 1857 : 44.
Antedon phalangium (part): Carpenter, 1888 : 158–165 [non-Mediterranean specimens.]; 1891 : 67.
Leptometra celtica: A. H. Clark, 1913*a* : 2; Gislén, 1947 : 3–4; Clark & Clark, 1967 : 564–572, fig. 32c–g; A. M. Clark, 1970 : 36–39, fig. 12; Sibuet, 1974 : 790–791.

MATERIAL. *Meteor* cruise 9c, st. 80a AT 17, 31°01′N, 10°16′W (off Morocco); 360–375 metres; 4 specimens.

Meteor cruise 9c, st. 82a KT 18, 31°35′N, 10°10·5′W: 180–145 metres; 38 specimens.

Meteor cruise 9c, st. 82b AT 19, 31°35′N, 10°10·5′W; 150–160 metres; 55 specimens.

Meteor cruise 9c, st. 90a AT 23, 37°22·8′N, 09°00·7′W (off Portugal); 170–150 metres; 18 specimens.

Meteor cruise 9c, st. 95 AT 29, 36°29·9′N, 11°33′W (Gettysburg Bank); 150–430 metres; 17 specimens.

Meteor cruise 9c, st. 120 KD 40, 36°40·7′N, 14°15·5′W (Josephine Bank); 211–218 metres; 51 specimens.

Meteor cruise 9c, st. 40/41, same coordinates; 198–293 metres; 19 specimens.

Meteor cruise 9c, st. 41, same coordinates; 234–241 metres; 13 specimens.

Meteor cruise 9c, st. 121a AT 42, 36°42′N, 14°14′W; 210–305 metres; 26 specimens.

Meteor cruise 9c, st. 123a AT 43, 36°42·3′N, 14°15·2′W; 231–210 metres; 26 specimens.

Meteor cruise 9c, st. 130 AT 48, 36°41·4′N, 14°14·8′W; 225–216 metres; 41 specimens.

Meteor cruise 9c, st. 130 BSN 13, same coordinates; 224–246 metres; fragments.

Meteor cruise 9c, st. 132 AT 50, 36°40·2′N, 14°17·5′W; 235–240 metres; 2 specimens.

Meteor cruise 19, st. 210 AT 128, 36°41′N, 14°16′W; 223–237 metres; 5 specimens.

Meteor cruise 36, st. 94 FD 141 or 96 FD 145, 24°58·3′N, 15°32·6′W; 25°25·7′N, 15°56·8′W (Western Sahara); 50 or 217–212 metres; 4 specimens.

Meteor cruise 36, st. 96 KT 144, 25°23·2′N, 15°58·7′W; 227–252 metres; 2 specimens.

Meteor cruise 36, st. 96 KG 512, 25°24·9′N, 15°59·2′W; 247 metres; 1 specimen.

Meteor cruise 36, st. 97 KT 146, 25°25′N, 16°00·9′W; 365–337 metres; 27 specimens.

Meteor cruise 36, st. 105 FD 157, 21°19·5′N, 17°29·2′W (Cap Blanc); 206 metres; 1 specimen.

Meteor cruise 36, st. 105 KT 158, 21°20·8′N, 17°29·5′W; 247–186 metres; 3 specimens.

Discovery st. 7977, 26°15′N, 14°43′W (between Canary Is and Western Sahara); 137–143 metres; several hundred specimens.

Apart from the specimens from Gettysburg Bank, most, if not all, of the specimens from any one station are immediately recognizable as having cirri of one of two forms. In the first (fig. 2a) the dorsal side of all but the proximal segments is more or less flared at the distal end so that the profile is slightly serrated, the penultimate segment having a distinct opposing spine. In the second (fig. 2b) the cirri are more slender and tapering, almost smooth in profile and no opposing spine is developed. The first corresponds to the key description of *L. celtica* by A. H. Clark (*in* Clark & Clark, 1967 : 553) and is particularly characteristic of the specimens from the Josephine Bank. The second approximates more to the description of *L. phalangium* (J. Müller) from the Mediterranean and is shown by the specimens from NW Africa and most of those from the Portuguese shelf; however, some of these Portuguese shelf specimens are intermediate, like those from the nearby Gettysburg Bank.

Similar observations of cirral form in Atlantic specimens of *Leptometra* have been made by Carpenter (1886), who noted that specimens from the Minch, between Scotland and the outer Hebrides, adjacent to the type-locality – the 'Sound of Skye' – are of the short, flared-segmented form in contrast to those from off Cape Sagres and Mondego, Portugal, whereas others from the Seine Bank (ENE from Madeira) Carpenter found show a wide range of form in the cirri. A. H. Clark confirmed Carpenter's observations on the same material. However, whereas Carpenter concluded that *L. celtica* should be treated as a dwarfed variety of *L. phalangium,* A. H. Clark considered that there is enough difference to maintain two species.

Gislén (1947) named as *L. celtica* specimens from the vicinity of Tangier in 130 metres depth with somewhat serrated cirri. However, he suggested that *L. phalangium* might occur outside the Mediterranean off the NW African coast at depths greater than this, being transported over the sill at the Gibralter Strait in the deeper westbound current from the Mediterranean.

Certainly the specimens now studied from Atlantic Morocco to Cap Blanc might well be

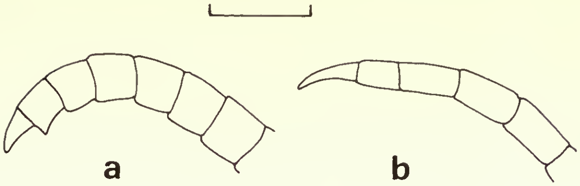


Fig. 2 *Leptometra celtica* (M'Andrew & Barrett). Tips of two extreme forms of cirri, a. *celtica*-form from Josephine Bank, b. *phalangium*-like-form from Morocco. The scale equals 2 mm.

identified as *L. phalangium* but the same is true of some but not all of those from Portugal. This fact and the presence of *celtica*-like specimens in the Gibraltar Strait and western Mediterranean deters me from adopting this course. Sibuet (1974) named as *L. celtica* specimens from the Alboran Sea, east of the Strait in the Mediterranean in 337–538 metres, though without comment on the form of their cirri.

Solution of this taxonomic problem might be assisted by study of material from SW Spain; also by detailed comparison of the particle size of the substrates with cirrus form. The specimens with longer straighter cirri would be expected on finer substrates.

Most specimens of this fragile species are more of less broken but one from the Josephine Bank (*celtica*-form) has almost complete arms just over 80 mm long. Its peripheral cirri are relatively short, up to only 22 mm or c. 25% of the arm length; they have 33–35 segments. P_1 and P_2 are very long and attenuated, c. 10 mm long and with 20–25 segments. This compares with cirrus and arm lengths of c. 35 and 50–60 mm in a *Discovery* specimen from NW Africa (*phalangium*-form), giving a value of c. 60%. It is notable that most of the specimens from off Western Sahara have a relatively high but rounded truncated centrodorsal, rather than the usual conical shape.

Trichometra cubensis (Pourtalès)

Antedon cubensis Pourtalès, 1869 : 214.

Trichometra delicata A. H. Clark, 1911*b* : 258; Clark & Clark, 1967 : 676–678.[?Non *T. delicata:* A. H. Clark, 1913*a* : 3, A. M. Clark, 1970 : 48, fig. 13.]

Trichometra cubensis: Clark & Clark, 1967 : 671–676; Meyer, Messing & Macurda, 1978 : 423. [?Non *T. cubensis:* A. H. Clark, 1923 : 11–12; A. M. Clark, 1970 : 46–48, fig. 17.]

MATERIAL. *Meteor* cruise 8, st. 8a AT 6; 37°39′N, 09°32′W (off Portugal); 1370–1430 metres; 8 specimens.

Meteor cruise 8, st. 19 AT 9, 33°34·4′N, 09°19·3′W (off Morocco); 1300 metres; 2 specimens.

Discovery st. 7711/66, 53°11·2′N, 20°05·1′W (far W from Ireland); 2432–2380 metres; 14 specimens.

Discovery st. 9029, 32°14·3–14·1′N, 11°2·8–2·5′W (off Morocco); 1886–1835 metres; 1 specimen.

Discovery st. 9042, 42°15·0–17·8′N, 11°22·0–19·7′W (off NW Spain); 1662–1541 metres; 14 specimens.

The largest specimens probably had arm length c. 55 mm, at which the arm width at the first syzygy is 1·5 mm.

The centrodorsal is blunt conical with a papillose dorsal pole. In one specimen the height just exceeds the diameter but the ratio of diameter/height ranges up to 1·7/1 with a mean of 1·3/1. The cirrus sockets usually number XLV–LXV and many specimens show complete regularity in their arrangement in columns, most often three in each radius. There is a more marked disparity in the size of the apical and peripheral cirri than is usual in most antedonids and the relative length of the segments decreases considerably with size. The small *Meteor* specimen with arm width at 3 + 4 only 0·8 mm has the longest cirral of peripheral cirri (the fifth) with length/median width 4·2/1 whereas in larger specimens with

Table 3 *Trichometra cubensis* (Pourtalès). Numerical data from one specimen from *Meteor* st. 8a (no. 19) and specimens from *Discovery* stations 7711 (nos 12–16) and 9042.

	Arms		Centrodorsal			Cirri		P_1		P_2		P_3	
No.	Width at 3 + 4	Length to 3 + 4	Diam.	Diam./Height	No.	Segs.	Length	Segs.	Length	Segs.	Length	Segs.	Length
1	1·5	4·5	3·5	1·5/1	LV	—	—	19	7·7	—	—	—	—
2	1·5	4·4	3·3	1·2	LX	—	—	—	—	13	5·0	—	—
3	1·5	4·2	3·1	1·3	LXV	—	—	18	6·2	—	—	—	—
4	1·5	4·2	3·2	1·3	LV	—	—	17	6·2	—	—	12	5·2
5	1·5	4·0	3·0	1·25	LV	—	—	—	—	—	—	—	—
6	1·4	4·6	—	—	XLVIII	42	18·5	15	6·2	14	6·6	11	5·8
7	1·4	3·8	2·7	1·4	L	—	—	—	—	—	—	—	—
8	1·25	3·3	—	—	LXV	38	16·2	12	4·2	13	4·4	12	5·0
9	1·2	3·8	2·4	1·1	XLVI	—	—	14	4·7	—	—	—	—
10	1·2	3·6	2·7	1·0	LVI	—	—	—	—	—	—	—	—
11	1·2	3·3	2·5	1·3	—	—	—	12	4·4	—	—	12	4·6
12	1·3	3·2	2·7	—	—	41	17·5	13	3·5	10	3·3	—	—
13	1·3	3·0	2·75	1·2	LXVI	—	—	16	5·0	11	3·7	10	3·5
14	1·25	3·2	—	—	—	40	19·5	15	4·9	12	3·6	10	3·6
15	1·2	2·9	—	—	—	37	—	12	3·3	—	—	10	3·2
16	1·2	2·75	2·25	1·3	LXIV	—	—	14	4·0	11	2·9	10	2·9
17	1·0	3·3	2·8	1·2	L	—	—	—	—	—	—	—	—
18	0·9	3·5	2·3	1·2	XLV	—	—	12	4·3	12	—	12	3·7
19	0·8	2·8	1·9	1·5	XLV	—	—	—	—	—	—	—	—
20	0·8	2·6	1·5	1·2	XLVI	—	—	11	3·3	8	2·2	8	2·5
21	0·7	2·5	1·25	1·25	—	25	8·0	10	2·7	—	—	—	—

arm width 1·2–1·5 mm the ratio is 1·6–2·7/1, on the few specimens where it can be measured, the cirri are so frequently all lost.

Larger specimens have the division series and arm bases approximating and distinctly flattened laterally, as described for West Indian specimens of *Trichometra cubensis* by A. H. Clark (*in* Clark & Clark, 1967), whereas *T. delicata* A. H. Clark from the Bay of Biscay and Portugal, in which the arm length is not known to exceed 40 mm, is similar to smaller specimens in having these ossicles rounded laterally. The division series, brachials and pinnulars mostly have flared and spinose distal edges. The distal intersyzygial interval is usually two muscular joints.

Most of the pinnules are broken; the longest intact P_1 found measures 7·7 mm and has 19 segments, whereas P_2 and P_3 in all but the smallest specimens have 10–14 and 10–12 segments respectively.

Affinities. The related species *Orthometra hibernica,* also small and with spinose distal ends to the brachials and pinnulars and recorded from W of Ireland to the Josephine Bank, W of Portugal, differs in having a much more flattened centrodorsal, without papillae, and appreciably shorter cirrals, even the longest less than half again as long as their median width.

Owing to the delicacy of this species and damage to the specimens collected, the fact that West Indian specimens have been recorded as having up to only 35 rather than 42 cirrals but as many as 25 rather than 19 pinnulars in P_1 is probably not significant. Nevertheless a direct comparison between specimens from the two sides of the ocean is desirable. The minimum depth recorded from the western tropical Atlantic is only 210 metres (Meyer, Messing & Macurda, 1978), compared with 1300 metres in the NE Atlantic, though SW of Iceland one *Ingolf* station was only 311 metres. A. H. Clark (*in* Clark & Clark, 1967) recorded as *T. cubensis* specimens from the area S of Newfoundland, W of Greenland and off Iceland, as well as in the West Indies. Meyer et al. have suggested that there may be two species-group taxa, a northern and a southern. Zoogeographically this idea has considerable justification and accordingly the references to the *Ingolf* specimens (either as *T. cubensis* or *T. delicata*) in the synonymy of *T. cubensis* given above are queried. The reference to the Helga specimen from west of Ireland as *T. delicata* by A. H. Clark (1913*a*) is additionally queried, having been referred to *Orthometra hibernica* by A. H. Clark (*in* Clark & Clark, 1967). However, since the cirri were described as having only 15–20 segments, the longest as much as three times as long as wide, I think this very unlikely and the specimen could after all have been a *Trichometra.*

One specimen from *Discovery* st. 7711 had its cirri clasped around the stalk of the hyocrinid *Anachalypsicrinus nefertiti.*

Antedonid sp. cf. *'Antedon' omissa* Koehler

Fig. 3

?*Antedon omissa* Koehler, 1909 : 268–269, pl. 32, fig. 10.
?*Thalassometra omissa:* A. H. Clark, 1950 : 184–185.

Material. *Discovery* st. 7984, 25°27′N, 16°10′W (off Western Sahara); 810–890 metres; 2 specimens.

Description. The larger specimen has ten arms 45 + ? c. 10 mm long, arm width at the first syzygy (Br3 + 4) 1·5 mm, length from the proximal edge of the IBr_1 to this syzygy 3·5 mm and to the second syzygy at 9 + 10 8·4 mm.

The centrodorsal is hemispherical, 3·0 mm in diameter and 1·8 mm high, a ratio of 1·7/1. The cirrus sockets number XXXVII and are spaced and irregularly arranged with long pointed papillae among them as well as on the apical area. The single remaining peripheral cirrus has 29 segments and is 15 mm long. The fifth and longest segment has length/median width 2·75/1; most of the cirrals are constricted medially and flared distally but the shorter distal ones have a dorsal crest, highest medially.

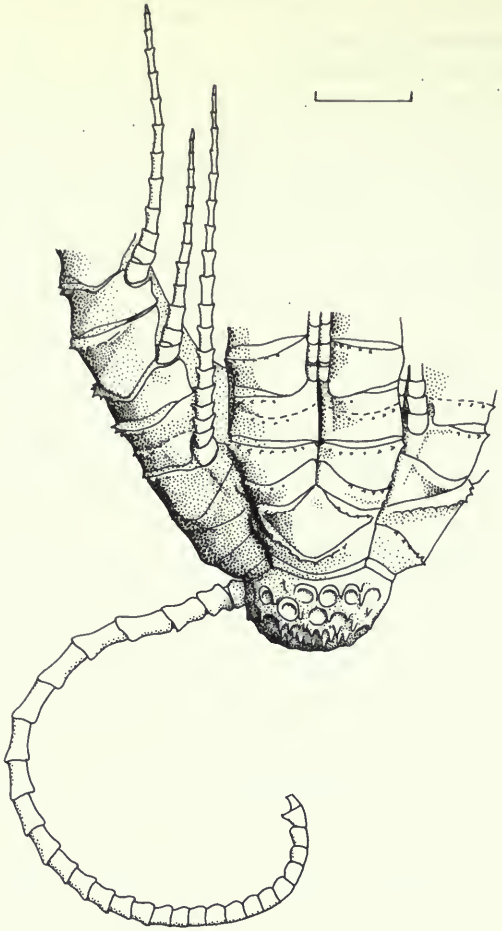


Fig. 3 Antedonid sp. cf. *'A.' omissa* Koehler. *Discovery* st. 7984. [The tip of the terminal claw is broken.] The scale equals 2 mm.

The ossicles of the division series have a small lateral flange each side; this and the arm bases are very sharply flattened laterally and the distal edges of the ossicles, even at the syzygies, bear fine pointed spines. The more distal brachials have spinose frills along their distal edges.

The second syzygy is at 9 + 10 in all but two cases, where it is at 7 + 8 or 12 + 13; the third syzygy is usually at 14 + 15 or 15 + 16; the distal intersyzygial interval is usually two muscular joints.

P_1, P_2 and P_3 have 19, 13 and 13 segments and measure 7·6, 5·8 and 6·0 mm. The first two pinnulars are short, the rest progressively more elongated. If breakage occurs it is usually after the second pinnular. P_4, sometimes P_3, is the first genital pinnule. The dorsal end of the distal edge of each pinnular is flared and bears a cluster of relatively elongated spines. The side plates in the pinnule ambulacra are partially rod-like with one or two proximal branches and a distal expansion into an irregular lattice. The covering plates are also inconspicuous and form an irregular lattice.

The smaller specimen is similar, though less spinose; it has lost all the cirri.

Affinities. These two specimens were taken at the same station with some much larger specimens of *Koehlermetra porrecta* from which they were distinguished by having only ten arms, a hemispherical rather than truncated centrodorsal with numerous pointed papillae, no transition segment in the single remaining cirrus, distinctly spinose division series as well as brachials and pinnulars and inconspicuous side and covering plates in the pinnules. At first they were thought to be *Trichometra cubensis,* collected from as close as Morocco (32°14′N), though the minimum depth for that species in the NE Atlantic appears to be 1300 metres, from the present records. *T. cubensis* too has ten arms, division series and arm bases somewhat flattened laterally in larger specimens (arm width at the first syzygy $>1{\cdot}2$ mm) and P_1 much the longest pinnule. However, all the specimens in the present collection referred to *T. cubensis* have blunt conical centrodorsals with papillae only on the apical area, XLV or more cirri (with at least 35 segments in the longest ones at arm width $>1{\cdot}2$ mm) arranged in fairly regular vertical lines, relatively longer division series and brachials (length to $3+4$ from the proximal edge of IBr_1 4·0–4·5 mm at width 1·5 mm, rather than only 3·5 mm), and only very fine bent rods in the pinnule ambulacra.

There is a possibility of identity with *Antedon omissa* Koehler, 1909, collected nearby SE of Tenerife, Canary Is in 1330–1340 metres, although Koehler referred this species to the Basicurva-group – the Thalassometrida – prompting A. H. Clark (1950) to include the species in *Thalassometra* itself. The single, poorly preserved specimen had the centrodorsal hemispherical, the division series slightly flattened laterally, the brachials flared and after about the seventh with spinose distal edges and P_1 much larger than P_2 (from the figure). However, nothing is said about papillae on the centrodorsal and the cirri are given as including only ten principal ones with others arranged above them, the number of cirrals being up to only 21; also P_1 and P_2 have only 12 and 6 segments and the distal intersyzygial interval is given as three to five muscular joints. The ambulacral plates are not described so affinity with the Thalassometrida cannot be certain. The only clue as to the size of the holotype of *A. omissa* is a disc diameter of 4 mm. The centrodorsal diameter would presumably be appreciably smaller than this, perhaps 2–3 mm.

In spite of the irregular position of the second syzygy occasionally, the two *Discovery* specimens appear to be referable to the Antedonidae and run down to the vicinity of *Trichometra* in the key to the subfamily Bathymetrinae by A. H. Clark (in Clark & Clark, 1967). This key is unfortunately far from satisfactory since it depends strongly on the relative cirral length and pinnular numbers, which vary to some extent with size. Hopefully more material will be forthcoming from the further collecting going on off NW Africa which should help towards a better assessment of the taxonomic position of these specimens.

METEOROMETRA gen. nov.

DIAGNOSIS. A genus of Antedonidae, subfamily Bathymetrinae* having a low hemispherical centrodorsal on which the cirri are more or less irregularly arranged and the dorsal pole is papillose; peripheral cirri with 17–25 segments, the longest ones flared distally and about twice as long as their median widths, the distal ones about as wide as long; the ossicles of the division series and arm bases are more or less constricted medially and flared and finely spinose distally; the pinnules all consist of attenuated segments after the first two short ones of each, the distal ends of the pinnulars being markedly flared and spinose; P_1 is markedly and consistently shorter and more slender than P_2 and the following pinnules.

TYPE SPECIES. *Meteorometra monticola* sp. nov.†

AFFINITIES. The hemispherical centrodorsal with cirrus sockets not regularly arranged, peripheral cirri mostly with more than 20 dorsally-flared segments and P_1 with usually 15–20 elongated segments ally *Meteorometra* with the genera included in the Bathymetrinae, of which *Orthometra, Hathrometra, Phrixometra* and *Trichometra* are recorded from certain parts of the Atlantic.

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* Since the taxa which have been included in the Bathymetrinae and Zenometrinae include all intermediate arrangements of the cirrus sockets and shapes of the centrodorsal from completely irregular on a low hemispherical ossicle in *Bathymetra* to well-marked vertical columns on a conical or columnar centrodorsal in *Zenometra*, I consider that these two subfamilies should be merged.

† *Monticola* – dweller on a mountain.

Orthometra with *O. hibernica* recorded below (p. 203) is easily distinguished by the low, flattened centrodorsal, lacking apical papillae, and the relatively numerous and short cirrals (25–32 in peripheral ones, the longest with length/median width less than 1·5/1).

Hathrometra with two species, *H. tenella* (Retzius) from NE America and *H. sarsi* (Düben & Koren) from Norway to Greenland (but not W or S of the British Isles), is a much more delicate genus with very attenuated cirri and P_1 much longer than P_2.

Phrixometra – predominantly a Southern Ocean genus though the type-species, *P. longipinna* (P. H. Carpenter), ranges N to the River Plate (c. 37°S, 54°W) – also has P_1 usually the longer pinnule, or at least it is similar in proportions to P_2, unlike that of *Meteorometra*; it is remarkable in being viviparous, females having brood pouches alongside the gonads. Also the division series and arm bases in *Phrixometra* are constricted and spaced laterally, not closely aligned.

Trichometra with a Hawaiian species as well as *T. cubensis* above, (p. 195), is probably the closest to *Meteorometra,* also having the centrodorsal papillose apically and most of the ossicles flared and spinose or rugose but again it differs in having P_1 stouter and more elongated than P_2, while the cirri and cirrals are more numerous (XL or more, the longest rarely with less than 30 segments).

The other bathymetrin genera with cirrals of comparable proportions include *Boleometra* (from Japan), *Nepiometra* (from the Philippines) and *Tonrometra* (from the East Indies and Southern Ocean). All these have P_1 larger than P_2 and indeed the reversal of proportions of these two pinnules in *Meteorometra* appears to provide a very basic distinction.

Meteorometra monticola sp. nov.

Fig. 4

Material. *Meteor* cruise 9a, st.-AT 88, 29°55′N, 28°20′W (Great Meteor Bank); 300 metres; 2 specimens.

Cruise 9c, st. 148a AT 55, 30°06·7′N, 28°27′W; 323–314 metres; 19 specimens.
Cruise 9c, st. 159a AT 60, 29°50·2′N, 28°29·8′W; 308–310 metres; 14 specimens.
Cruise 9c, st. 172 BSN 24, 29°47·9′N, 28°23·3′W; 300–310 metres; 1 specimen.
Cruise 9c, st. 180a AT 77, 30°01·1′N, 28°24′W; 315–320 metres; 6 specimens.
Cruise 9c, st. 186 KT 82, 29°55·9′N, 28°35′W; 308–330 metres; 1 specimen.
Cruise 9c, st. 189 KT 84, 30°05·1′N, 28°38·4′W; 340–305 metres; 2 specimens.
Cruise 19, st. 126 DD 90/91, 30°09·5′N, 28°29·5′W; 342–357 metres; 1 specimen.
Cruise 19, st. 129 AT 96, 30°01·5′N, 28°30′W; 292 metres; 5 specimens.
Cruise 19, st. 131 AT 97, 30°08′N, 28°38·5′W; 330–473 metres; 8 specimens.
Cruise 19, st. 133 DD 100, 29°49·5′N, 28°19·5′W; 315–326 metres; 1 specimen.
Cruise 19, st. 133 AT 101, 29°48·5′N, 28°22·5′W; 306–308 metres; 3 specimens.
Cruise 19, st. 134 AT 104, 29°46′N, 28°29′W: 320–620 metres; 3 specimens.
Cruise 19, st. 136 KT 106, 29°59·5′N, 28°23′W: 307–337 metres; 2 specimens.
Cruise 19, st. 137 KT 107, 30°03′N, 28°23′W; 307–337 metres; 2 specimens.
Cruise 19, st. 140 AT 109, 30°03′N, 28°33·5′W; 295–310 metres; 2 specimens.
Cruise 19, st. 157 KT 115, 29°55·5′N, 28°30′W; 292–297 metres; 5 specimens.
Cruise 19, st. 157 KT 116, 29°58′N, 28°20′W; 322–422 metres; 4 specimens.
Cruise 19, st. 163 KT 123, 30°09·5′N, 28°32·2′W; 307–337 metres; 1 specimen.
Cruise 19, st. 164 KT 124, 30°06′N, 28°28·4′W; 307–317 metres; 2 specimens.

Type material. All the specimens are small and more or less broken. The holotype is the best specimen from cruise 19, st. 157 KT 115; the paratypes are the others from this sample and the specimens from cruise 9c, sts 148a, 180a and 189, most of which are included in table 4.

Description. The holotype is specimen 7 in table 4. The arms are all broken by 27 mm and may not have measured more than 40 mm when complete.

The centrodorsal is hemispherical, diameter/height 1·9/1·1 mm = 1·7/1; the cirri are

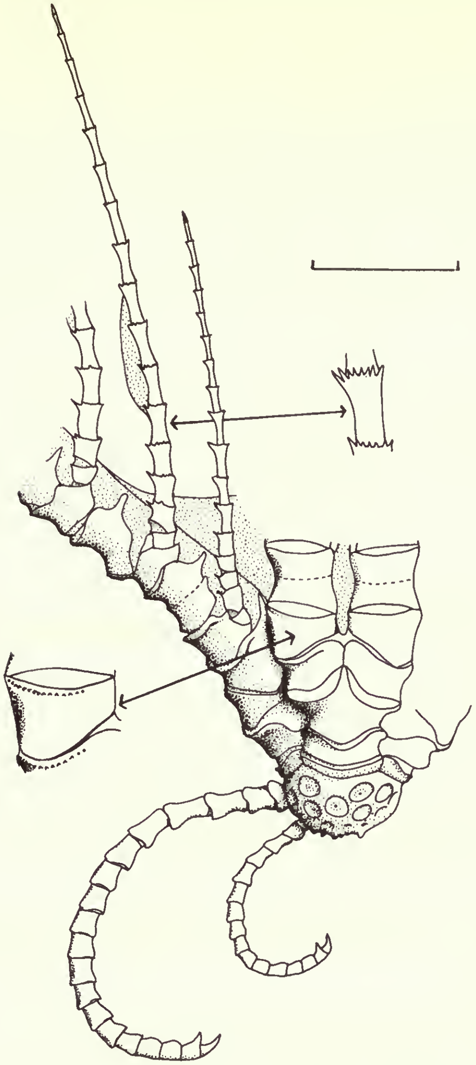

Fig. 4 *Meteorometra monticola* gen. & sp. nov. Centrodorsal from specimen 13 in table 4, *Meteor* st. 148a, otherwise from the holotype, st. 157, with enlargements of a brachial and a pinnular to show the ornamentation. The scale for the main figure equals 2 mm.

irregularly arranged around the sides and the apical area is papillose. There appear to be only c. XXV cirri, the minimum observed in the type series. The peripheral ones have 19–23 segments of which the fourth and longest has length/median width up to 2·0/1.

The ossicles of the division series and arm bases are markedly constricted medially and flared distally, where they are armed with very fine close serrations. Beyond the arm bases these serrations become coarser, fewer and more spaced, elongating into spines. The second syzygy is usually at Br9 + 10 and the distal intersyzygial interval is two, occasionally three, muscular joints.

The first pinnule is markedly more slender and somewhat shorter than P_2 and the following pinnules; P_2 is the first genital pinnule. After the first two short segments, the remaining pinnulars become progressively more attenuated; the distal ends of all but the terminal one are markedly flared and spinose. The frequent breaking point for the distal pinnules is after the second pinnular. There appear to be no rudiments of side or covering

Table 4 *Meteorometra monticola* gen. & sp. nov. Numerical data from 20 specimens from *Meteor* cruise 9c, sts 148a, 180a and 189 and cruise 19, st. 157 (the holotype, no. 7).

	Arms		Centrodorsal		Cirri									
								P_1		P_2		P_3		Length
No.	Width at 3 + 4	Length to 9 + 10	Diam.	Diam/Ht	No.	Max. Segs	Length	Segs	Length	Segs	Length	Segs	Length	P_2/P_1
1	0·95	6·5	2·0	1·8/1	XXXIII	23	9·0	17++	c. 6	23	10·0	19+2, 3	c. 9·5	1·7/1
2	0·90	6·5	2·2	1·9	XXXIII	25	10·0	21	6·2	19+1, 2	c. 9·5	20	9·3	1·5
3	0·90	7·1	2·0	1·8	XXIX	21	8·0	18	6·0	—	—	13	5·2	—
4	0·90	6·4	2·0	2·0	XXX	24	9·6	—	—	17+2, 3	c. 8	16	6·2	—
5	0·90	6·4	2·0	1·8	XXXV	—	—	—	—	—	—	19	8·1	—
6	0·85	6·7	2·2	1·7	XXX	—	—	—	—	—	—	—	—	—
7	0·85	6·8	1·9	1·7	c. XXV	23	8·3	18 + 1?	c. 6	18	7·7	12	5·7	1·3
8	0·85	6·7	1·7	1·9	XXVIII	23	7·7	—	—	—	—	—	—	—
9	0·85	6·0	1·7	1·9	XXIX	—	—	—	—	16	7·2	13	6·0	—
10	0·80	6·2	1·8	2·0	XXXIII	—	—	15 + 1, 2	c. 5	20	8·7	14	6·7	1·7
11	0·75	6·2	—	—	—	23	7·5	16++	c. 5	16 + 1, 2	c. 8	12	5·2	1·6
12	0·75	6·1	1·9	1·6	c. XXX	—	—	17	5·7	24 + 1, 2	c. 11	15	7·1	1·9
13	0·75	6·2	1·8	2·1	XXX	24	9·2	20	6·0	17 + 1, 2	c. 8	16 + 2, 3	c. 7·5	1·3
14	0·75	5·8	1·8	2·3	XXVII	23	8·7	—	—	—	—	14	5·8	—
15	0·75	5·7	1·7	—	—	22	8·0	—	—	19	8·7	17	6·7	—
16	0·75	5·7	—	—	—	23	—	—	—	19	7·5	—	—	—
17	0·75	5·8	1·5	1·4	—	18	—	15	4·6	15 + 2, 3	c. 7	13	4·3	1·5
18	0·70	5·8	—	—	—	21	6·7	16	4·3	17	6·4	12	4·7	1·5
19	0·60	4·6	1·3	—	—	19	5·8	13	3·3	13	4·7	10	3·9	1·4
20	0·60	4·7	1·1	1·6	c. XXV	17	—	—	—	13	4·5	12	4·0	—
Ranges	0·60–0·95	4·6–7·1	1·1–2·2	1·4–2·3	XXV–XXXV	17–25	5·8–10·0	13–21	3·3–6·2	13–25	4·5–11·0	10–20	3·9–9·5	1·3–1·9

plates in the pinnule ambulacra, but on the disc the ambulacra are bordered by opaque plates.

PARATYPES. The maximum arm length was probably c. 50 or perhaps 55 mm.

The mean diameter/height of the centrodorsal in 15 specimens is 1·8/1. In the largest specimens the longest cirrals are relatively slightly shorter than in the holotype, with length/median width c. 1·8/1. Some of the cirrus sockets in most specimens are arranged in vertical lines but this is much less regular than in the specimens referred to *Trichometra cubensis.* P_1 is always markedly smaller than P_2, the mean inverse length ratio in ten specimens being 1·5/1. The two largest specimens (1 and 2 in the table) give an idea that P_3 increases allometrically with respect to P_2 since the lengths of these two pinnules are almost the same, where the smaller specimens tend to have a P_2/P_3 length ratio of 1·2–1·5/1.

Several samples included also material of the hydroid *Polyplumaria flabellata* G. O. Sars, which range from the Congo (Zaire) N to Iceland in 30–800 metres. I am indebted to Dr. P. F. S. Cornelius for this information. Some specimens have their cirri clasping branches of a gorgonian.

DISTRIBUTION. On present evidence *Meteorometra monticola* appears to be endemic to the Meteor Sea-mount but it is also likely to occur on the nearby Cruiser Sea-mount (c. 32°N, 28°W) and, like *Cyathidium foresti* (see p. 209), found on the slopes of the Meteor Bank, may even be found around the islands of the Azores at a similar depth of c. 300 metres, though the greater part of the Azores Plateau exceeds 1500 metres.

Orthometra hibernica (A. H. Clark)

Trichometra hibernica A. H. Clark, 1913*a* : 2–3.
Orthometra hibernica: Clark & Clark, 1967 : 680–682; A. M. Clark, 1970 : 34–36, fig. 11. [Non *O. hibernica:* A. H. Clark, 1923 : 57 = *Heliometra glacialis*].

MATERIAL. *Meteor* cruise 9c, st. 111 KD 39; 36°53·3′N, 14°24·7′W (Josephine Bank, W of Portugal); 960–980 metres; 1 specimen.

Although the arms are all detached from the first syzygy, some of the proximal pinnules remain intact and allow a description of these appendages for the first time. The arm width at 3 + 4 is 0·75 mm and the length to 9 + 10 5·75 mm. The total arm length probably did not exceed c. 20 mm.

The centrodorsal is very low, as in the paratype figured in 1970. The longer cirri have c. 30 short segments, most with a rounded transverse dorsal 'ridge' which is approximately median on the very short distal segments.

The division series and proximal brachials have finely serrated distal edges; on the remaining brachials the fine spines become fewer but longer.

Some proximal pinnules are as follows:
P_1 with 13 segments is 3·2 mm long
P_2 with 12 segments is 2·7 mm long; another with 11 segments is 2·5 mm
P_3 with 10 segments is 2·7 mm and is slightly thicker, likewise
P_4 with 10 segments 2·5 mm.
The first two pinnulars are short but the following ones become attenuated and are flared and spinose at their distal ends. The more distal pinnules are probably relatively longer with more expanded joints.

DISTRIBUTION. This record provides an extension of range to the south from the Bay of Biscay NW from Brittany and confirms a maximum depth of more than 750 metres; it is otherwise known only from W of Ireland (53–54°N, 11½°W, 698–749, ?914, metres).

Family PENTAMETROCRINIDAE

Pentametrocrinus atlanticus (Perrier)

Eudiocrinus atlanticus Perrier, 1883*b* : 725; Koehler, 1909 : 271–274, pl. 32, figs

Eudiocrinus (Pentametrocrinus) atlanticus: Koehler & Vaney, 1910 : 31.
Pentametrocrinus atlanticus: A. H. Clark, 1913*a* : 4; 1923 : 44; Mortensen, 1927 : 24, fig. 11; Clark & Clark, 1967 : 790–794; Messing, 1978: 700–708, figs 1–5, 8–11, 13–16; Meyer, Messing & Macurda, 1978 : 423.
Pentometacrinus atlanticus: Cherbonnier, 1970*a* : 343, 348.
Pentametacrinus atlanticus: Cherbonnier, 1970*b* : 1266, 1268.

MATERIAL. *Discovery* st. 7967, 29°20′N, 12°15′W (NE of Lanzarote, Canary Is); 1576–1539 metres; 1 specimen.

Discovery st. 8519/7, 24°02′N, 16°59′W (off Western Sahara); 1037–994 metres; 15 specimens.

Discovery st. 8931; 24°58·8′–25°05·4′N, 16°31·1–32·2′W; 955–1012 metres; 1 specimen.

Discovery st. 9042, 42°15·0–17·8′N, 11°22·0–19·7′W (off NW Spain); 1662–1541 metres; 3 specimens.

As usual all the specimens collected of this distinctive five-armed species are more or less badly broken. One of the largest (from st. 9042) has the centrodorsal diameter 4·0 mm and height 2·0 mm, the shape being low hemispherical. All the LXVIII cirri are broken. In contrast, a specimen from st. 7967 with centrodorsal diameter/height 3·2/1·3 mm and almost discoidal in shape, has only XIX cirrus sockets in one irregular peripheral ring. Messing gives a range of the diameter/height ratio from 1·4–3·6/1 and a maximum cirrus number of c. XC so clearly there is a great range in the centrodorsal shape and cirrus number.

A detached cirrus 20 mm long from st. 8519 has 18+ segments, the distalmost one broken so at least one more when intact; length/width of the fourth and longest segment is 2·3/0·4 mm or nearly 6/1. There is also a more slender complete detached cirrus 21·5 mm long with 19 segments. A. H. Clark (*in* Clark & Clark, 1967) gave the maximum cirral number as 17 and maximum length as 35 mm but Messing (1978) queried the length as an error of interpretation.

Three specimens from st. 8519 are unusual in having the first pinnule sometimes *before* the first syzygy (brachials 4 + 5); two of them have a P_1 on the right side of Br_2 and a P_a on the left of Br_3 on one arm only, while the third has a P_a on the left of Br_3 on two arms. The centrodorsal diameter in these three is 3·1, 2·75 and 2·6 mm and their arm widths at 4 + 5 are 1·75, 1·5 and 1·5 mm respectively. Otherwise the first pinnule is P_2 on Br_5, as usual in *P. atlanticus.* Only *P. varians* (P. H. Carpenter) from the Maldive area to Japan regularly has P_1 and P_a present.

These localities are within the known range of the species which extends in the NE Atlantic from SW of Ireland to NW of Africa and in the W Atlantic from off Martinique (Lesser Antilles) to the Blake Plateau N of the Bahamas.

Thaumatocrinus jungerseni A. H. Clark

Thaumatocrinus jungerseni A. H. Clark, 1915 : 149, 150; 1923 : 13–17, figs 2–4; Clark & Clark, 1967 : 782–785.

MATERIAL. *Discovery* st. 7711/57, 52°53·3′N, 19°52′W (far W from southern Ireland); 2742–2734 metres; 6 specimens.

Discovery st. 7711/62, 52°50·0′N, 20°02·8′W; 2727–2720 metres; 18 specimens.

Discovery st. 7711/85, 53°05·8′N, 19°55·7′W; 2652–2626 metres; 2 specimens.

The specimens collected of this distinctive species with its ten unbranched arms arising from ten radials are more or less badly broken, particularly with regard to the cirri. However, some of the *Discovery* specimens exceed in size the type-material from the *Ingolf* collections from W of Iceland for which the maximum arm length was estimated by A. H. Clark (1923) as 110 mm and the centrodorsal diameter 3·0 mm. A specimen from *Discovery* st. 7711/85 has several arms almost intact, measuring c. 130 + ?c. 5 mm; since this has the centrodorsal diameter 3·0 mm and the arm width at the first syzygy (4 + 5) 1·4 mm, a larger broken specimen with these measurements 4·4 and 1·7 mm may have had arms as much as 200 mm long.

Table 5 *Thaumatocrinus jungerseni* A. H. Clark. Numerical data from ten specimens from *Discovery* st. 7711/62 and one (no. 7) from st. 7711/85.

Arms				
Width at 4 + 5	Length to 4 + 5	Centrodorsal diameter	Cirrus number	No.
1·7	4·2	4·4	XVII	1
1·3	4·25	3·0–3·3	XIII	2
1·5	3·8	3·3–3·6	XVI	3
1·3	4·2	3·1	IX	4
1·6	3·75	3·1	XIII	5
1·4	3·9	2·9–3·3	XIV	6
1·4	3·8	3·0	XVIII	7
1·2	3·75	3·7	XIV	8
1·25	3·75	3·2	XIV	9
1·2	3·75	2·5–2·9	X	10
1·0	3·3	2·25–2·4	XI	11

The size of the peripheral cirri is very variable and some of the sockets are markedly projecting so that the outline of the centrodorsal is often rather irregular, resulting in a range of diameter according to the aspect, as given for some specimens in table 5. All the cirri are broken at or before the fifth cirral. The larger cirri of larger specimens have length/median width of the first three cirrals less than 1/1. In the tenth specimen in table 5 this ratio in a stout cirrus is 1·0/1, while the smallest (last) specimen in the table has even its stoutest cirrus with a third cirral ratio of 1·5/1 and a slender one with as much as 3·2/1. As I noted in 1967 (*in* Clark & Clark), the relative length of the proximal cirrals, as well as the number of cirri, vary too much for a practicable distinction between *T. jungerseni* and *T. renovatus* P. H. Carpenter from the Southern Ocean (near the Crozet Is, S of Australia and off the Antarctic continent). However, the position of the first genital pinnule will probably serve to distinguish betwen them. In *T. renovatus* this pinnule is P_a, P_2 or P_b, whereas in the *Discovery* specimens of *T. jungerseni* it is usually P_3 or P_c, sometimes P_4 and only rarely P_b.

A few specimens have the proximal pinnules intact; the largest in table 5 has the segment number and length of P_1, P_2 and P_3 : 34, 10·0 mm; 22, 9·1 mm and 32, 12·1 mm, P_3 being the first genital pinnule. A specimen with width at the first syzygy 1·4 mm gives counts of 22, 7·1 mm, 24, 7·9 mm and 23, 8·3 mm.

It should be noted that the position of the first arm syzygy is rather variable in this material. In c. 50% of cases it is at Br4 + 5 but may also be at 3 + 4 or 5 + 6. One specimen was seen to lack P_1 on seven of the ten arms.

DISTRIBUTION. These new records provide an extension of range somewhat to the southward in the North Atlantic, the type material being from the Denmark Strait and from SW of Iceland (c. 62°N, 30°W); the depth range is slightly extended beyond 2075 metres to 2734 metres.

Family **BATHYCRINIDAE**

Democrinus parfaiti Perrier

Democrinus parfaiti Perrier, 1883*a* : 450–451; Gislén, 1938 : 28–29; 1947 : 7–9, fig. 3; Roux, 1977 : 39–40, figs 4, 9, 10, 11, 16, pl. 2, figs 6–8, pl. 5, figs 1–6; A. M. Clark, 1977 : 172–177, fig. 3.

MATERIAL. *Meteor* cruise 36, st. 127 FD 181; 33°40′N, 08°55′W (off Morocco); 988 metres; 1 specimen lacking arms beyond the first brachial.

Table 6 *Bathycrinus gracilis* Wyville Thomson. Numerical data from the 7 *Meteor* specimens for comparison with table 1 of A. M. Clark (1977); no. 5 is from st. 24, no. 2 from st. 30 and the rest from st. 38. The height of the radials cited is the mid-radial side view (i.e. slightly foreshortened).

Calyx:	1	2	3	4	5	6	7
Height (basals and radials)	—	1·7	2·0	—	—	—	—
Basals height	—	0·50	0·58	—	—	—	—
Basals lower width	—	0·70	0·75	—	—	—	—
Radials height	1·08	1·10	1·46	1·50	1·75	1·90	2·42
Radials lower width (A)	0·75	0·83	0·92	1·42	1·67	1·42	1·50
Radials upper width (B)	1·83	1·90	2·25	3·25	3·33	3·25	3·83
A as % B	41	44	41	44	50	44	39
Post-radial series:							
Crown length (incl. radials)	c. 18	18+	20+	—	20++	c. 40	c. 65
IBr$_1$ and $_2$ length	2·42	2·60	3·00	3·42	3·58	3·75	4·33
IBr$_{1-2}$ width	1·33	1·42	1·50	—	2·58	2·33	2·92
IBr$_1$–Br$_4$ length	5·08	5·58	6·20	7·10	7·70	7·70	8·60
Br$_{4+5}$ width	0·58	0·67	0·71	0·92	1·17	0·87	1·21

Bathycrinus gracilis Wyville Thomson
Fig. 5

Bathycrinus gracilis Wyville Thomson, 1872 : 772–773; P. H. Carpenter, 1884*b* : 243–245, fig. 16, pl. 8a, figs 1–3; Koehler, 1909 : 254; A. M. Clark, 1977 : 164–167, fig. 1a–f.

Material. *Meteor* cruise 3, st. 24, 42°17·2′N, 14°46·3′W (W of Cape Finisterre); 5270 metres; 1 crown.

St. 30 AT 3, 42°55·4′N, 14°07·9′W; 5260 metres; 1 specimen, missing most of the stalk.

St. 38 AT 5, 42°10·7′N, 14°20·8′W; 5275 metres; 4 crowns and one specimen missing most of the stalk.

This collection has at last yielded well-developed specimens (unfortunately only two) of *Bathycrinus gracilis* in which the basal ring is still attached to the radials and the crown is not in process of regeneration. Sadly no more than 11 proximal columnals remain, all of them discoidal.

In both these specimens the junction between radial and basal rings tends to form an angle of c. 150°, the basal ring itself tapering downwards slightly but to a much less marked degree than the radials. The degree of splay of the radial ring can be expressed by the angle off the vertical derived from the vertical height and top and bottom diameters of the ring. It ranges from 24–31° in the seven specimens from the *Meteor* compared with 30 and 31° in the two *Chain* specimens included in table 1 of A.M.C. (1977) and 30–37° in the three specimens of *B. aldrichianus* in the same table. Angles of 26½°–32° are obtained for the three specimens of *B. aldrichianus* for which Macurda & Meyer (1976) cite measurements of the top diameters of both basal and radial rings, although the degree of splay appears to be greater in the crown shown in their fig. 1A. (Unfortunately they only cite measurements of the lower widths of individual radials of their detached crowns, some of which were of larger size – maximum radial ring diameter 2·41 mm compared with 1·56 mm for the largest one with basal ring attached.)

Macurda & Meyer note that the basal ring in *B. aldrichianus* is only partially fused, sutures being distinguishable in the lower part. The same is true in the specimen of *B. gracilis* from *Meteor* st. 30. Absence of fusion of the basal ring in the adult has been supposed by Gislén (1938) to be characteristic of *Monachocrinus* A. H. Clark, 1917, which is also supposed to differ from *Bathycrinus* in having a curved rather than angular junction between radial and basal rings, as well as in having non-muscular and muscular joints regularly alternating throughout the arms. These characters are discussed and doubt thrown on their generic weight in a paper on stalked crinoids now in the press (A. M. Clark, Rec. Aust. Mus.).

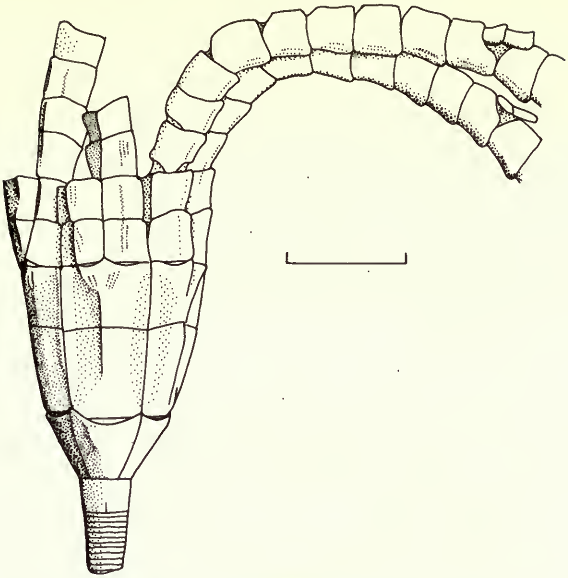

Fig. 5 *Bathycrinus gracilis* Wyville Thomson. *Meteor* st. 30. The scale equals 2 mm.

The *Meteor* specimens agree closely with the two crowns taken SW from Ireland by the *Chain* and described in 1977 (A. M. Clark), having low but sharp keels and lateral flanges on the division series and first brachials, giving way to fluting on the following ossicles, which are flared at their distal ends, making a slightly serrated profile to the arm (fig. 5).

Though indistinct, the non-muscular joints are usually at 1 + 2, 4 + 5, 7 + 8, 10 + 11 and then alternate regularly with muscular joints but one arm of the third specimen in table 6 appears to have 1 + 2, 6 + 7 + 8, 9 + 10 + 11. Because of variations in the positions of these joints, the first pinnule may be on brachial 10 or 12, though it is usually on Br11. Out of 38 arms intact to the first pinnule, in 24 it is at Br11, in 9 at Br12 and in 5 at Br10. Since Macurda & Meyer record their specimens of *B. aldrichianus* as having the first pinnule from Br8 to Br11, the mean position of this pinnule may justify maintaining distinction of these two taxa at the specific level. No other differences in the calyx or crown are evident but it is possible that material of *B. gracilis* with intact stalks will reveal differential characters.

DISTRIBUTION. Apart from the record from off the U.S.A. of *Bathycrinus serratus* A. H. Clark, 1908, reduced to a synonym of *B. aldrichianus* by A. H. Clark (1949), all the records of crowns or intact specimens which can confidently be referred to *B. aldrichianus* are from the equatorial or South Atlantic in 3300–5600 metres. *B. gracilis* is recorded from SW of Ireland (c. 50°N), between the Azores and Portugal (c. 39°N, 21°W) and now from W of northern Spain, in 4430–5275 metres, which appears to show a distribution limited to the West European Basin. However, the absence of intermediate records may be an artefact of collection, considering the great depths involved.

Family **PHRYNOCRINIDAE**

Zeuctocrinus gisleni A. M. Clark

Zeuctocrinus gisleni A. M. Clark, 1973 : 277–281, fig. 5, pl. 2; Roux, 1977 : 34, figs 6, 7, pl. 1, figs 6–8, pl. 3, figs 1–7.

MATERIAL. *Discovery* st. 8511/2, 41°49′N, 11°06′W (off NW Spain); 2574–2584 metres; 1 specimen.

DISTRIBUTION. This record provides a small extension of range SW from Roux's *Thalassa* sample in the southern Bay of Biscay (c. 44°N, 8°W) and takes the depth range beyond the 2380–2432 metres of the type (and only other known) locality, W of Ireland (c. 53°N, 20°W).

Porphyrocrinus thalassae Roux

Porphyrocrinus thalassae Roux, 1977 : 34–38, figs 1B, 2, 3, 5, 11A, 12, 13, 14, 16B, pl. 1, figs 1–5, pl. 7, figs 1–6, pl. 8, figs 1–6, pl. 9, figs 1–6; A. M. Clark, (in press).

MATERIAL. *Discovery* st. 8511/2, 41°49′N, 11°06′W (off NW Spain); 2574–2584 metres; 1 specimen.

The contemporaneous discovery by the *Thalassa* and *Discovery* of this species with its secondary arm branching comparable with that of *Phrynocrinus nudus* A. H. Clark from Japan, helps to justify the synonymizing with Phrynocrinidae by Roux (1977) of the nominal family Porphyrocrinidae, which I split off from the Bathycrinidae in 1973 to accommodate *Porphyrocrinus* Gislén and *Naumachocrinus* A. H. Clark on the basis of their fused plate rather than dendritic stalk attachment. In 1977 (p. 168) I noted that this character alone is not of sufficient weight to justify a family distinction, prompted by new observations on stalk attachments in the Bathycrinidae. Partly on the basis of the fine structure of joints, Roux also cast doubt on my grouping of *Zeuctocrinus*, in which the second post-radial ossicle is a primary axillary, with *Phrynocrinus*, where any axillaries are secondary, irregular and asymmetrical, rather than with *Bathycrinus*. This may well be important but at the same time the absence of discoidal proximal columnals in fully grown specimens of *Zeuctocrinus* forms a strong resemblance to *Phrynocrinus*. Possibly even Phrynocrinidae should be merged with Bathycrinidae, as Roux (1977) implied, though in his summary classification of the order Millericrinida (1978) he listed Phrynocrinidae including the four genera mentioned in this discussion. Clearly further study is needed on the affinities of these taxa to settle the best disposition.

Further remarks on *Porphyrocrinus thalassae* will be published in the proceedings of the 1978 Conference on Echinoderms in Sydney (A. M. Clark, Rec. Aust. Mus. [in press]).

DISTRIBUTION. This record extends the range slightly SW from the type-locality in the Bay of Biscay (c. 44°N, 07°W).

Family **HYOCRINIDAE**

Gephyrocrinus grimaldii Koehler & Bather

Gephyrocrinus grimaldii Koehler & Bather, 1902 : 68–79; Koehler, 1909 : 256–264, pl. 1, fig. 12, pl. 32, figs 1–9; Roux, 1977 : 31.

MATERIAL. *Discovery* st. 9042, 42°15·0–17·8′N, 11°22·0–19·7′W (off NW Spain); 1541–1662 metres; 3 specimens.

A transparency by Dr P. J. Herring verifies Koehler's observation of the colour (1909) as bright yellow in life.

DISTRIBUTION. This locality is intermediate between those of the type material, near the Canaries and Madeira and the *Thalassa* record from the Bay of Biscay (c. 49°N, 11°W) and is also within the known depth range of 1470 (?1420) – 1970 metres.

Appendix

For the sake of complete coverage of the *Meteor* crinoid collections, the following record of a species of the relict genus *Cyathidium* from the Great Meteor Bank, admirably described by Fechter (1973), should be mentioned. Sadly the going to press of this paper overlapped with that of a prior description of the same species by Cherbonnier & Guille (1972) based on material from the Azores in 380–900 metres.

Family **HOLOPODIDAE**

Cyathidium foresti Cherbonnier & Guille

Cyathidium foresti Cherbonnier & Guille, 1972 : 2193–2196, pl. 1.
Cyathidium meteorensis Fechter, 1973 : 162–169, figs 1, 2.

MATERIAL. *Meteor,* 1967, st. 173, 29°42·2′N, 28°20·5′W (Great Meteor Bank); 850–580 metres.

St. 178, 29°57·9′N, 28°15·7′W; 690–610 metres. A total of 20 specimens.

Acknowledgements

I am indebted to Dr H. Fechter of the Zoologische Sammlung des Bayerischen Staates, Münich and Dr A. L. Rice of the Institute of Oceanographic Sciences, Wormley, for access to the material.

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A new abyssal genus of the family Ophiuridae (Echinodermata : Ophiuroidea)

Gordon L. J. Paterson

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Introduction

A new genus of abyssal ophiuroid from the NE Atlantic belonging to the subfamily Ophiurinae of the family Ophiuridae is described. Its relationship to the genera *Ophiotrochus* and *Bathylepta* is discussed and justification given for the transfer of these two genera from the Ophioleucidae to the Ophiurinae, both of which are rediagnosed. *Uriopha* is the fourth purely abyssal genus belonging to the family Ophiuridae to have been discovered in recent years, *Perlophiura* Belyaev & Litvinova, 1972, *Abyssura* Belyaev & Litvinova, 1976 and *Bathylepta* Belyaev & Litvinova, 1972 are the other three. It is perhaps slightly surprising that a new genus should be found in what could be considered a well investigated region. This might be due to the small size of the specimens resulting in their being overlooked by past researchers. The specimens of *Uriopha* form part of a collection of deep sea ophiuroids made by the Institute of Oceanographic Sciences' *Discovery* Investigations off North West Africa.

Systematic descriptions

URIOPHA gen. nov.

Diagnosis. A genus of the subfamily Ophiurinae, family Ophiuridae, with the disk completely covered by granules obscuring the plates beneath; the disk is convex or even domed; no arm combs or genital papillae are developed; the jaw has a spiniform apical papilla flanked on each side by oral papillae which becomes more blocklike distally; the adoral plates are long and thin; the oral shields are small and triangular; the second oral tentacle pore emerges superficially, away from the mouth slit; the tentacle pores are round, distinct and occur along the whole arm length, each has one large rounded scale and sometimes a smaller indistinct scale underlying it; there are two conical appressed arm spines on each lateral arm plate beyond the disk.

Type-species. *Uriopha ios* sp. nov.

Derivation of name. *Uriopha* is an anagram of *Ophiura*, a genus of the Ophiuridae, and *ios* is derived from the initials of the Institute of Oceanographic Sciences.

Uriopha ios sp. nov.

Fig. 1

The eleven individuals of the type series have disk diameters of 3–4 mm. Viewed from above the disk is round to subpentagonal; in side view it appears high and in many specimens domed. A dense coating of granules, each about 0·04 mm in diameter, covers the dorsal surface and ventral interradial areas, obscuring the plates, including the oral and adoral shields but not the oral plates. The underlying dorsal plates are numerous, small and slightly imbricated, more so in the domed specimens. Except for the centrodorsal plate in some specimens, the primary rosette is usually indistinct. The radial shields are irregular though

Bull. Br. Mus. nat Hist. (Zool.) **38** (4): 211–218 Issued 25 September 1980

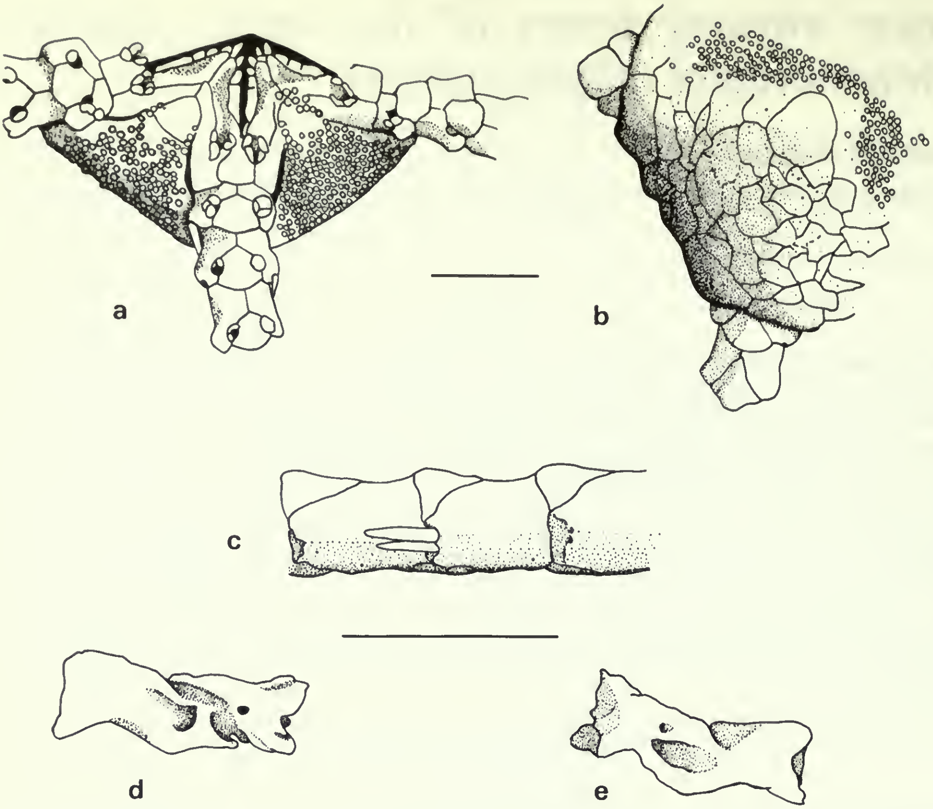

Fig. 1 *Uriopha ios* sp. nov. (a) Holotype, (b–e) Paratypes. (a) Ventral view of part of disk. (b) Dorsal view of part of denuded disk. (c) Lateral view of arm fragment. (d) Adradial and (e) abradial view of oral plate. Bar scales = 1 mm..

approximately rectangular in shape, length: maximum breadth is 1·5–2·0 : 1. They may be wholely contiguous or only distally so. Interradially the radial shields are separated by several plates. Arm combs are absent. Ventral disk scales are slightly larger and not imbricated like those of the dorsal surface.

The apical papilla is spiniform; on each side of it are 3 or 4 oral papillae, broadening progressively from peglike to blocklike. The oral plates are long and rectangular and are raised up in the interradial midline where they meet. The adoral plates meet on the midline although this suture is partially obscured by the oral shield; they are approximately four times longer than wide, flaring distally where they meet the first lateral arm plates. The oral shield is triangular with a straight distal side; it partially overlies the adorals and is totally proximal to the two genital slits, not spanning them.

The second oral tentacle pore arises superficially and away from the mouth slit and is surrounded on three sides by 4–6 tentacle scales, arising partly from the first ventral arm plate and partly on the bordering edge of the adoral plate. These scales are distinct from and do not form a continuous series with, the mouth papillae; in some cases they may appear continuous but there is a distinct gap between the last oral papilla and the nearest tentacle scale (see Fig. 1a). The genital slits are edged by granules not differentiated from those of the disk.

The fragile arms are almost cylindrical, slightly higher than wide. They are often broken off short. The first dorsal arm plate is overlaid by the disk; it is contiguous with the next plate but subsequent plates are separated becoming progressively smaller down the arm. The first complete dorsal arm plate is trapezoidal with a convex distal edge, subsequent plates are triangular with a slight convex edge. In side view the dorsal arm plates appear swollen above the lateral arm plates (see Fig. 1c). The two arm spines are conical situated towards the ventral end of the lateral arm plates. The first ventral arm plate is pentagonal sometimes with a cleft or furrow running proximally into the mouth slit. The following plates are pentagonal with the lateral edges indented by the tentacle pores, the distal edge is slightly convex. The tentacle pores are round, distinct and present on all the arm segments. The tentacle pore of the first arm segment has two, sometimes three tentacle scales, the remaining pores have one distinct rounded scale sometimes with one small indistinct scale.

The holotype (fig. 3) has a disk diameter of 3·4 mm. The arms of the holotype and paratypes are all broken but from one specimen which has an almost intact arm, measuring 5·5 mm, it can be estimated that the arms were two to three times the disk diameter. Type locality: Stn 8524 1, *Discovery* Investigations, 20°46′N : 22°42′W (west of Cap Blanc and north of Cape Verde Islands), 4412 m.

Discussion. The superficial position of the second oral tentacle pore prompts inclusion of this genus in the subfamily Ophiurinae, the second subfamily, Ophiolepidinae differs in having this opening within the oral slits. *Uriopha* shows a combination of characters which readily distinguish it from the other genera of the Ophiurinae. Certainly some individual characters unusual in this subfamily, such as the low number of arm spines or the granulation of the disk, are shared by particular genera, suggesting possible relationships, but these are unsupported by the other characters. For example, the genera *Ophiomastus* Lyman, 1878, *Ophiopyrgus* Lyman, 1878 and *Ophiuraster* H. L. Clark, 1939 also have a low number of arm spines, two or less, and a simple form of tentacle scale on the arm pores but they have large thick and sometimes swollen disk and arm plates and in the case of *Ophiomastus* and *Ophiopyrgus* the disk is dominated by the centrodorsal, primary rosette and radial shields. *Uriopha* by contrast has small thin disk and arm plates and the primary rosette is indistinct. The genital slits also differ, being long and well developed in *Uriopha* but short or absent altogether in these three genera, while the shapes of the adoral and oral shields are very different and only *Uriopha* possesses a granulated disk.

However, *Uriopha* does appear to have a genuine affinity with the genus *Ophiotrochus* Lyman, 1878, referred by Matsumoto (1915) to the Ophioleucidae when he differentiated that family from the Ophiuridae (Ophiolepidae in Matsumoto's terminology) (see Fig. 2). Both have a similar arrangement and number of arm spines, with two arm spines set on the ventral end of the lateral arm plate, though *Ophiotrochus* has more than two arm spines on the first arm segments; both have similar tentacle pore and scale form on the free arms, though *Uriopha* has two to three scales on the first arm pore; the genital slits are developed to a similar degree; the adoral and oral shields are of similar shape and arrangement and both have granulated disks though in *Ophiotrochus* this is limited to the ventral side.

This affinity does not imply inclusion of the new genus in the Ophioleucidae since several factors support a proposition that not only *Ophiotrochus* but also *Bathylepta* Belyaev & Litvinova, 1972, should be transfered from the Ophioleucidae to the Ophiurinae. First and most importantly, the second oral tentacle pore arises superficially outside the mouth slit whereas the other ophioleucid genera have the second oral tentacle pore opening entirely within the mouth slits. The alignment of this pore is the primary character of the Ophiurinae and alone warrants their distinction from the Ophioleucidae. Within the order Chilophiurina, comprising the families Ophiodermatidae, Ophionereididae, Ophiocomidae, Ophiuridae and Ophioleucidae, only the Ophiurinae possesses this character. Koehler (1904) first noted its importance and suggested that it might be used to separate groups within the genus *Ophioglypha* (*Ophiura, sensu* H. L. Clark, 1911). In his revised classification of the Ophiuroidea, Matsumoto (1915, 1917) regarded the alignment of the second oral pore as an important character at the family–subfamily level. In his parallel keys to the family groups of the Chilophiurina (Matsumoto, 1915, pp. 74–75) this character separates his Ophiomastinae, now Ophiurinae, from all the other family-group units. Although the second oral tentacle of the Ophiurinae emerges ventrally in basically two ways,

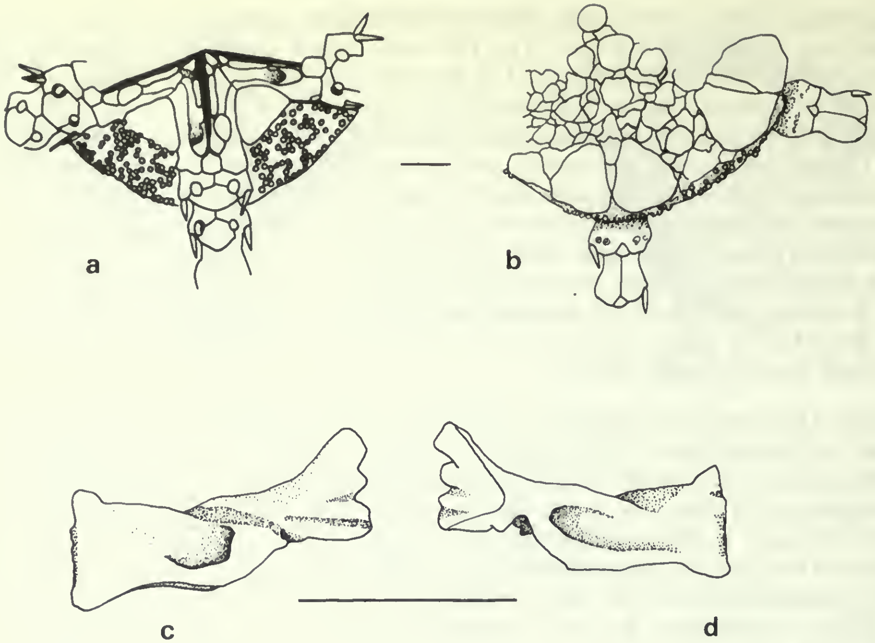

Fig. 2 *Ophiotrochus longispinus* H. L. Clark. (a) Ventral and (b) dorsal view of part of disk. (d) Adradial and (c) abradial view of oral plate. Bar scales = 1 mm.

either opening via a slit or directly on to the ventral surface, both Koehler (1922) and Matsumoto (1915, 1917) consider them to be variations of one character. Such a distinct character suggests that the relationships between the subfamilies Ophiurinae and Ophiolepidinae should be investigated and further study may warrant raising them to family status. In addition *Ophiotrochus* and *Bathylepta* lack the large contiguous successive dorsal and ventral arm plates, the well developed peg-like oral papillae and the long flattened arms characteristic of the Ophioleucidae. These two genera currently form an anomalous group within the Ophioleucidae not closely related to *Ophioleuce* Koehler, 1904 and the other genera included.

One character thought by Fell (1960) and Matsumoto to be important but now set aside is that of the insertion and degree of integration of the arms with the disk. This character seems to be affected by both the extent of the genital slit and the state of preservation of the specimen and may be misleading. Matsumoto (1917) considered *Ophiotrochus* to be a neotenous ophioleucid probably because of the ventral insertion of the arms even though he noted that the second oral tentacle pore emerges superficially, unlike that of the other genera of the Ophioleucidae.

Bathylepta is related to both *Uriopha* and *Ophiotrochus* by the reduced number of arm spines and the development and shape of the adoral and oral shields. It differs mainly in the juvenile form of the oral papillae, which could be interpreted as a neotenous condition, the absence of genital slits and of tentacle scales except on the second oral tentacle pore (see Belyaev & Litvinova, 1972; Madsen, 1977).

Due mainly to the work of Schoener (1967, 1969) on post larval development of several species of deep water ophiuroids, we are better able to recognize neotenous characters prolonged from early ontogenetic stages. Her observations indicate that such features as the lack of tentacle scales, the rudimentary form of the oral papillae and the lack of genital slits in *Bathylepta*; the fused oral papillae in *Ophiotrochus* and the small non-contiguous dorsal arm plates in *Bathylepta* and *Uriopha* and probably their absence in *Ophiotrochus*, are all characters found in the early stages of most species. As ontogeny progresses the tentacle scales appear. Also the superficial adradial edge of the oral plate differentiates into a

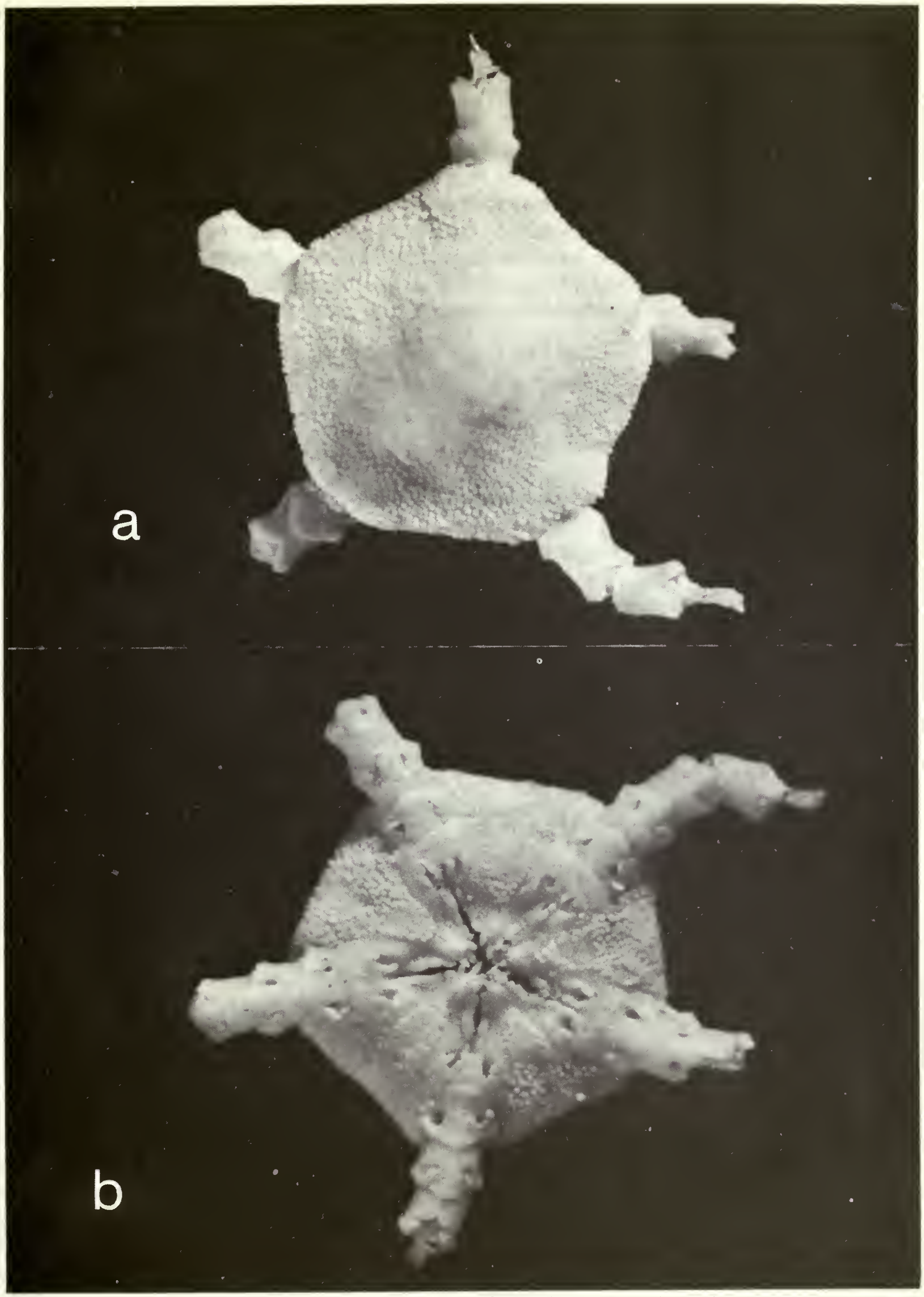

Fig. 3 *Uriopha ios* sp. nov. (a) Dorsal and (b) ventral view of holotype.

flange which subsequently enlarges and becomes indented to form individual oral papillae. Further development varies with the species, in some, such as *Ophiura ljungmani*, the papillae separate from one another and become peglike, whereas in *Ophiomusium lymani* they remain contiguous and block-like. As the dorsal arm plates enlarge, in many cases they become contiguous while in others they remain small and separate. By a disk diameter of c. 2–3 mm the adult features are recognisable and further growth involves only minor changes in proportions. Schoener showed that in *Ophiura sarsi* the juvenile stages up to 0·9 mm disk diameter have only two arm spines, rather than the adult three, suggesting that this character in the genera under discussion may be a neotenous condition; however, I have been unable to confirm this for the juvenile stages of any other ophiuroid species.

The removal of *Bathylepta* and *Ophiotrochus* from the Ophioleucidae leaves the family more homogenous and allows the following more restricted definition:

OPHIOLEUCIDAE Matsumoto, 1915

A family of the Chilophiurina with the disk comprised of scales completely or partially covered by a coat of granules sometimes also covering the radial shields, adoral and oral shields; the adoral shields are usually long and flared distally; the oral shields are small, triangular or arrow shaped; the teeth are papilliform and arranged in a single series; the second oral tentacle pores open within the mouth and are not visible externally; the arms are long, flat and wide and taper slowly to the end of the arm; the dorsal and ventral arm plates are large and successive ones are contiguous, at least proximally; the tentacle pores are variable in size, sometimes enlarged but becoming smaller distally, armed with one to several scales; the disk may appear superficial, overlying the arm bases.

The familly as restricted includes the genera *Ophioleuce,* Koehler 1904, *Ophiernus* Lyman 1878, *Ophiocirce* Koehler, 1904, *Ophiopyren* Lyman 1878 and *Ophiopallas* Koehler 1904 (*Ophioperla* Koehler, 1912 was inexplicably and erroneously referred to the Ophioleucidae from the Ophiuridae by Fell, 1960 and followed by Spencer & Wright, 1966. Later Fell, 1961, moved *Ophioperla* back to the Ophiurinae).

The Ophiurinae can be defined as follows:

OPHIURINAE Lyman, 1865

A subfamily of the Chilophiurina with a disk covered by scales, which are usually distinct but may be obscured by a covering of opaque skin or granules; the primary rosette is often conspicuous, sometimes dominating the disk; the radial shields are usually conspicuous; opposite each arm base a comb of papillae or spinelets is often present and may be continuous ventrally with papillae bordering the genital slits; the oral and adoral shields are variously developed (though ill-defined in the specialized genus *Astrophiura*); the teeth are narrow, pointed or papilliform; at the apex of the jaw no tooth papillae are present but usually a single infradental papilla bordered on each side by a continuous series of pointed, rounded or blocklike papillae; the second oral tentacle pore opens either directly or via a slit onto the ventral surface; the arms are of moderate or short length, widest proximally, tapering, flat or cylindrical, usually not moniliform, the exceptions being *Ophiotrochus* and *Perlophiura* which possess moniliform arms; the lateral arm plates are very evident, the dorsal and ventral arm plates being usually small so that successive ones are contiguous only on the basal segments, in some cases the dorsal arm plates may be undeveloped altogether as in *Anthophiura* and *Ophiotrochus*; the arm spines are mostly small and appressed; the tentacle pores are of varying sizes and may be found throughout the arm length or only proximally, usually armed with rounded or spine-like scales, which are absent in *Haplophiura,* the tentacle scales are variable in number and arrangement; the disk may appear to surround the arm bases.

The genera belonging to this subfamily are as listed by Fell (1960) with the following additions: *Anophiura* H. L. Clark, 1939, *Ophioperla, Perlophiura, Abyssura, Ophiotrochus, Bathylepta,* and *Uriopha.*

Uriopha, Ophiotrochus and *Bathylepta* are compared and contrasted in table 1. While these three genera form a distinct closely-related group within the Ophiurinae, further study is needed before their relationships to the remaining genera in this subfamily can be clarified.

Table 1 Comparing the genera *Bathylepta, Ophiotrochus* & *Uriopha.*

Character	*Bathylepta*	*Ophiotrochus* (see fig. 2a–d)	*Uriopha* (see fig. 1a–e)
Area of granulation on disk	Total	Ventral only	Total
Arm spine number	2	4 on first arm joint past the disk then 2	2
Adoral shields	Well developed	Well developed	Well developed
Oral shield	Small triangular	Small triangular	Small triangular
Genital slits	Absent	Present	Present
Dorsal armplate	Present, triangular	Absent	Present, triangular
Radial shields	Long thin not contiguous	Wider than long contiguous or distally so	Wider than long contiguous or distally so
Oral papillae	Very neotenous	Wide, blocklike, fused	Peglike becoming block-like distally
2nd oral tentacle pore	With 2 small scales	With one large fused opercular plate	With 4–6 scales
Tentacle scales of arms	Absent	One large round scale	One large round scale

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A revision of the spider genus *Macopaeus* (Araneae : Salticidae)

F. R. Wanless

Department of Zoology, British Museum (Natural History) Cromwell Road, London SW7 5BD

Introduction

The genus *Macopaeus* Simon, 1900 formerly included three species. The type species *M. spinosus* Simon belongs in the subfamily Lyssomaninae and is clearly related to *Asemonea* O. P.-Cambridge and *Pandisus* Simon. The original description of *M. spinosus* was based on a female, but Simon (1900) did not indicate the number of specimens examined. A female type specimen was examined by Roewer (1965) who diagnosed the genus but did not provide a description of the species. Despite the fact that this specimen has been subsequently lost and that the epigyne has never been figured, the spines on leg I are arranged in a distinctive manner and it is possible to identify the species with reasonable certainty. The other two species *M. madagascarensis* Peckham & Peckham from Madagascar, and *M. celebensis* Merian from Celebes are not related to *M. spinosus,* but belong in the genus *Brettus* Simon which has recently been revised by the author (Wanless, 1979).

In the present paper *Macopaeus* is redefined; *M. spinosus, Brettus celebensis* comb. n., and *B. madagascarensis* comb. n., are described and figured; and a neotype is designated for *M. spinosus.* The measurements were made in the manner described by Wanless (1978).

Genus *MACOPAEUS* Simon

Macopaeus Simon, 1900 : 381. Type species *Macopaeus spinosus* Simon, by original designation and monotypy. Simon 1901 : 394, 397, 399. Merian, 1911 : 303. Petrunkevitch, 1928 : 181. Roewer, 1954 : 932; 1965 : 6. Bonnet, 1957 : 2684.

DEFINITION. Spiders of medium size (4·0–8·0 mm). *Carapace:* longer than broad, moderately high with elevated eye region (Fig. 1A, C); fovea long, sulciform, positioned midway between posterior lateral eyes and posterior thoracic margin. *Eyes:* with black surrounds except anterior medians; disposed as in figure 1A; all relatively large; posterior ocular quadrangle longer than broad, entire quadrangle about 50% of carapace length. *Clypeus:* moderately high, slightly concave. *Chelicerae:* of medium size, more or less vertical; promargin with 4 teeth, retromargin with 8. *Maxillae:* of medium length, blades rounded, outer lateral margins slightly excavated; slightly divergent. *Labium:* subtriangular, about half maxillae length, lateral margins slightly excised basally. *Sternum:* cordiform. *Pedicel:* short. *Abdomen:* elongate ovoid; spinnerets of medium length, anteriors robust, medians and posteriors slender; tracheal system not examined. *Legs:* long and slender; legs I with robust ventral spines on metatarsi and distal half of tibiae; other leg spines less robust, more scattered on legs II and less numerous on legs III and IV; claws pectinate, tufts present. *Female palp:* long and slender. *Epigyne:* openings distinct, spermathecae large; vulva not examined.

A fuller definition can only be given when the male is discovered and additional material becomes available for study.

AFFINITIES AND DIAGNOSIS. *Macopaeus* evidently belongs in the subfamily Lyssomaninae and seems to lie near *Asemonea* and *Pandisus*, two closely related genera both of which are known from Madagascar. It is separated from *Pandisus* by the large posterior median eyes, and from *Asemonea* by having the posterior ocular quadrangle longer than broad.

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Macopaeus spinosus Simon
(Fig. 1A–F)

Macopaeus spinosus Simon, 1900 : 381, ♀, Madagascar, Antongil (MNHN, Paris) [not examined, presumed lost]. Simon, 1901 : 396, 399. Petrunkevitch, 1928 : 181. Roewer, 1954 : 932; 1965 : 6. Bonnet, 1957 : 2684..

REMARKS. Roewer (1965) examined, but did not describe the type specimen of this species which has been subsequently lost. The specimen described below agrees more or less with the original description (Simon, 1900) and with subsequent remarks made by Simon (1901) in respect of leg I spination, and is here formally designated neotype.

DIAGNOSIS. *M. spinosus,* known only from the female is separated from all other known lyssomanids by the disposition of the eyes and structure of the epigyne (Fig. 1A, E).

MALE. Unknown.

FEMALE NEOTYPE. *Carapace* (Fig. 1A, C): pale amber with brownish marginal bands and faint bands extending from posterior lateral eyes to near posterior thoracic margin; thinly clothed in short amber hairs with iridescent violet hairs in eye and foveal regions. *Eyes:* fringed by whitish hairs that are iridescent under some angles of illumination. *Clypeus:* sparsely covered in pale amber hairs. *Chelicerae:* yellow-brown, shiny; thinly clothed in amber hairs; promargin with 4 teeth, retromargin with 8. *Maxillae and labium:* whitish yellow to pale yellow. *Sternum* (Fig. 1F): whitish yellow; glossy, with scattered pale amber hairs. *Coxae:* subequal in size; pale yellow. *Abdomen:* whitish yellow with black markings; thinly clothed in fine iridescent pale amber hairs; spinnerets pale yellow. *Legs:* pale yellow to light amber with sooty lateral markings; legs I (Fig. 1B) with strong spines, those on the tibiae restricted to distal half of segment. *Epigyne* (Fig. 1E): vulva not examined.

Dimensions (mm): total length 5·6; carapace length 2·32, breadth 1·84, height 1·36; abdomen length 3·2; eye row widths, anterior medians 1·2, anterior laterals 1·48, posterior medians 0·8, posterior laterals 1·0; quadrangle length 1·2. *Ratios:* AM : AL : PM : PL : 15 : 9·5 : 6 : 8; AMM : CL (clypeus) : 15 : 6.

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. Neotype ♀, Madagascar, Beanana, ii. 1970 (*A. Lambillon,* MT. 142.599 part) (MRAC, Tervuren).

Brettus celebensis (Merian) comb. n.
(Fig. 2A–D)

Macopaeus celebensis Merian, 1911 : 304, ♀. Holotype ♀, Celebes, Wald bei Duluduo (NM, Basel, 88a) [Examined]. Roewer, 1954 : 932. Bonnet, 1957 : 2684.

AFFINITIES AND DIAGNOSIS. *B. celebensis* is closely related to *B. anchorum* Wanless from India, but may be distinguished by the relatively short and wide seminal ducts (Fig. 2C). The presence of dense dorsal fringes on tibiae I (evidently lacking in *B. anchorum*) may also be a useful diagnostic character.

MALE. Unknown.

FEMALE HOLOTYPE. *Carapace* (Fig. 2A, D): dark brownish orange; clothed in recumbent short white hairs. *Eyes:* with black surrounds except AM; anteriors fringed in whitish hairs. *Clypeus:* clothed in whitish hairs. *Chelicerae* (Fig. 2B): brownish orange; clothed in pale brown hairs; promargin with 3 teeth, retromargin with 6 or 7. *Maxillae:* orange to yellow-Orange with median brown markings. *Labium:* brown tipped yellow-orange. *Sternum:* brownish orange with darker margins, shiny; clothed in fine whitish hairs. *Coxae:* unequal in size, I and IV slightly largest; brownish orange. *Abdomen* (detached, shrunken and partly rubbed): brown-black, clothed in recumbent pale yellowish hairs, iridescent under some angles of illumination. *Legs:* brown to yellow-brown; clothed in fine whitish iridescent hairs

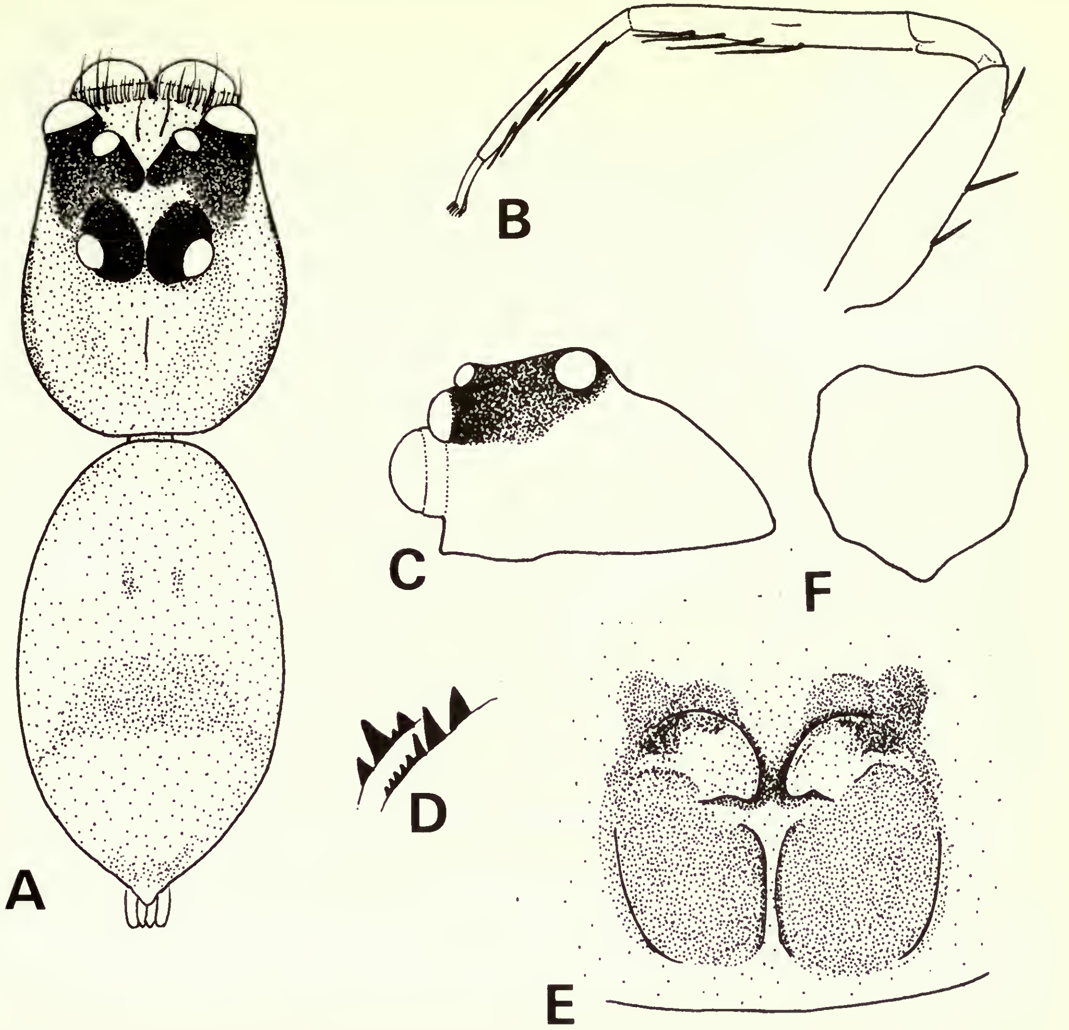

Fig. 1 *Macopaeus spinosus* Simon, neotype ♀: A, dorsal view, B, leg I; C, carapace, lateral view; D, cheliceral teeth, inner view; E, epigyne; F, sternum.

with dense grey-black ventral fringes on femora I, patellae I and tibiae I, also dense dorsal fringes on tibiae I; spines strong and numerous. *Palps:* long and slender; pale brown to whitish yellow. *Epigyne* (Fig. 2C): very similar to that of *B. anchorum*, but the ducts are wider and do not extend to the posterior margin of the somewhat rectangular opening; vulva not examined.

Dimensions (mm): total length about 6·6; carapace length 2·96, breadth 2·28, height 1·6; abdomen length 3·6; eyes, anterior row 1·48, middle row 1·04, posterior row 1·28; quadrangle length 1·2. *Ratios:* AM : AL : PM : PL : 14 : 7·5 : 5 : 6; AL – PM – PL : 7·5 – 11; AM : CL (clypeus) : 14 : 6.

DISTRIBUTION. Celebes.

MATERIAL EXAMINED. Holotype ♀, data given in synonymy.

Brettus madagascarensis (Peckham & Peckham) comb. n.
(Fig. 3A–D)

Macopaeus madagascarensis Peckham & Peckham, 1903 : 182, ♀. Holotype ♀, Madagascar (MCZ, Harvard) [Examined].

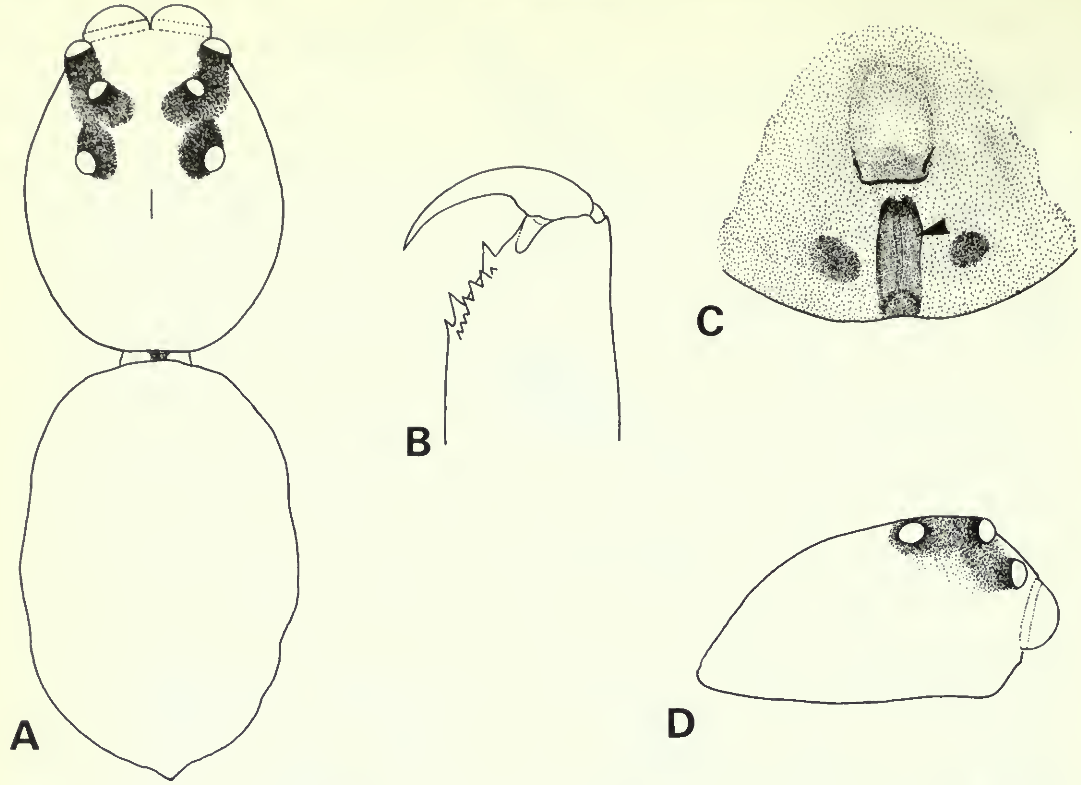

Fig. 2 *Brettus celebensis* (Merian), holotype ♀: A, dorsal view; B, chelicera; C, epigyne; D, carapace, lateral view.

M. madagascariensis: Roewer, 1954 : 932; 1965 : 6. Bonnet, 1957 : 2684. [Unjustified emendation].

AFFINITIES AND DIAGNOSIS. *B. madagascarensis* is a distinctive species readily separated from other known species of *Brettus* by the structure of the epigyne (Fig. 3C) and distribution.

MALE. Unknown.

FEMALE HOLOTYPE. *Carapace* (Fig. 3A, D): brown with margins and eye region clothed in recumbent short white hairs (long bright red hairs in eye area, described in the original description are no longer evident). *Eyes:* with black surrounds except AM; anteriors fringed in whitish hairs. *Clypeus:* clothed in whitish hairs. *Chelicerae* (Fig. 3B): yellow-brown with sooty markings; irregularly clothed in short whitish and long yellow-brown hairs; promargin with 3 teeth, retromargin with 5. *Maxillae and labium:* yellow-brown to light brown. *Sternum:* pale brown, shiny. *Coxae:* unequal in size, I and II largest; pale brown to brown. *Abdomen* (detatched, shrunken and partly rubbed): brown-black; irregularly covered in recumbent short whitish hairs, iridescent under some angles of illumination. *Legs:* mostly detached and broken, I and II missing; generally dark brown to yellow-brown; spines moderately strong and numerous. *Palps:* missing. *Epigyne* (Fig. 3C): vulva not examined.

Dimensions (mm): total length about 4·4; carapace length 2·2, breadth 1·76, height 1·27; abdomen length 2·04; eyes, anterior row 1·16, middle row 0·8, posterior row 1·0; quadrangle length 0·96. *Ratios:* AM : AL : PM : PL : 10·5 : 6 : 4·5 : 5; AL – PM – PL : 6 – 8; AM : CL : 10·5 : 4.

DISTRIBUTION. Madagascar.

MATERIAL EXAMINED. Holotype ♀, data given in synonymy.

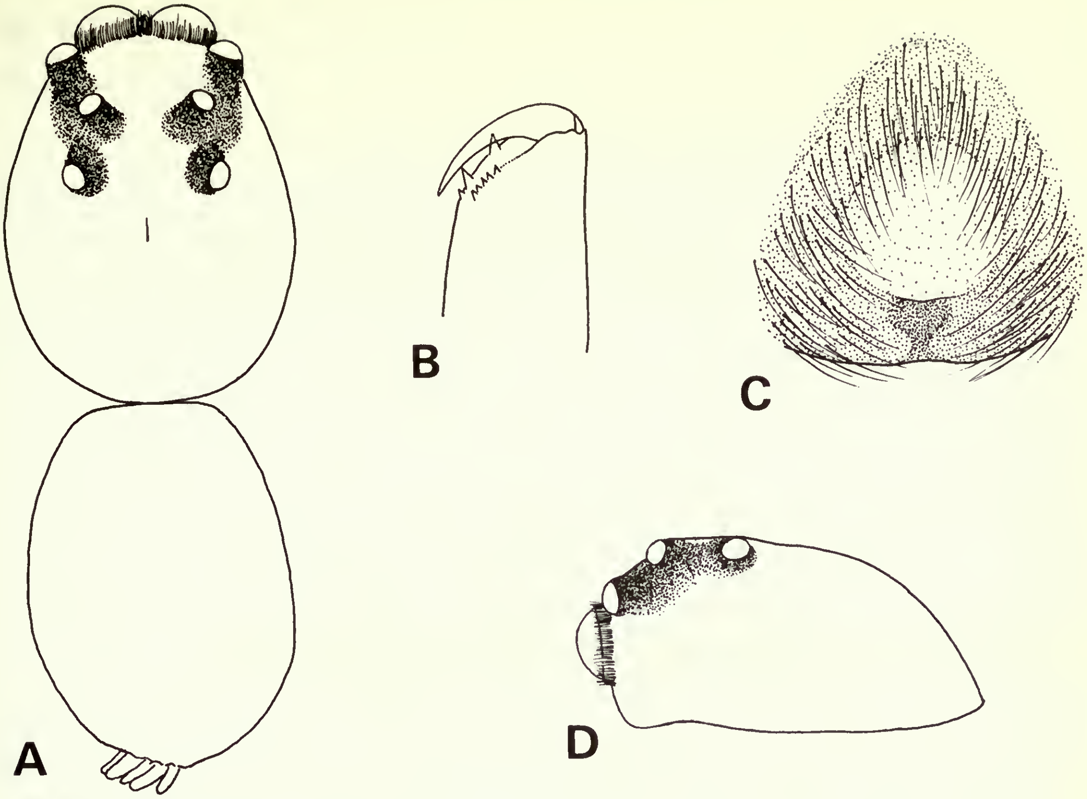

Fig. 3 *Brettus madagascarensis* (Peckham & Peckham), holotype ♀: A, dorsal view; B, chelicera; C, epigyne; D, carapace, lateral view.

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A revision of the spider genus *Orthrus* (Araneae : Salticidae)

F. R. Wanless

Department of Zoology, British Museum (Natural History) Cromwell Road, London SW7 5BD

Introduction

The genus *Orthrus* Simon 1900, known only from Borneo and the Philippines, is comprised of three known species, two of which are described here as new. The genus was formerly placed in the salticid subfamily Lyssomaninae on account of somatic similarities with *Asemonea* Simon and *Onomastus* Simon. Furthermore, *Orthrus* and *Onomastus* were considered to form a link between lyssomanines and ordinary salticids "Les genres *Onomastus* et *Orthrus* font le passage des *Asemonea* aux Salticides ordinaires" (Simon, 1901). *Onomastus* and *Asemonea,* which are at present being revised by the author, evidently belong in the Lyssomaninae, but *Orthrus* shows no close affinities with lyssomanine spiders. Galiano (1976) in a review of lyssomanine genera also expressed doubts about the systematic position of *Orthrus* and, unfortunately, its affinities with other salticid subfamilies is uncertain as the genitalia are relatively simple and of the kind often found within the family.

Although the biology of *Orthrus* species is poorly known, they are considered to be active spiders which hunt their prey over vegetation. In some respects they resemble lyssomanines: females and juveniles of *O. muluensis* sp. n., are green in life and have been collected from the underside of leaves, a habitat often frequented by New World Lyssomanines. Curiously, nothing appears to have been published on the habitat or behaviour of Old World species.

The measurements were made in the manner described by Wanless (1978), but for the leg spination the system adopted is that used by Platnick & Shadab (1975).

Genus *ORTHRUS* Simon

Orthrus Simon, 1900 : 28. Type species *Orthrus bicolor* Simon, by original designation and monotypy. Simon, 1901 : 395, 398, 400. Petrunkevitch, 1928 : 181. Roewer, 1938 : 78, 1954 : 932. Bonnet, 1958 : 3215. Galiano, 1976 : 60, 66, 67.

Definition. Small to medium spiders ranging from about 3·8 to 4·8 mm in length. Species sexually dimorphic, males with porrect, elongate chelicerae and sometimes with distinct colour markings; not hirsute, but fringes often present on male palps and legs I. *Carapace:* moderately high, longer than broad, fovea moderately long, positioned just behind posterior lateral eyes; microsculpturing not marked; cuticle weakly irridescent (under some angles of illumination). *Eyes:* with black surrounds except anterior medians, surrounds sometimes edged in whitish or pale yellow guanin; anterior row more or less contiguous, apices recurved in frontal view; posterior median eyes relatively small, slightly nearer to anterior laterals than to posterior laterals; posterior row narrower than anterior row; quadrangle length between 49 and 53% of carapace length. *Clypeus:* low. *Male chelicerae:* of different shapes, porrect, elongate; fang long; promargin with 3 or 4 teeth, retromargin with 6 or 8. *Female chelicerae:* of medium size, slightly inclined anteriorly; promargin with 3 teeth, retromargin with 7. *Maxillae:* elongate, divergent. *Labium:* tongue-shaped, slightly longer than broad, slightly less than half maxillae length. *Sternum:* scutiform. *Coxae:* subequal in females, coxae I largest in males. *Pedicel:* short. *Abdomen:* elongate, sometimes tapered; scuta lacking; spinnerets moderately long and slender, subequal in length; tracheal system not

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examined (insufficient material). *Legs:* long and slender; fringes of short stiff hairs sometimes present on male legs I; spines moderately strong to weak, less numerous on posterior legs; claws pectinate; tufts present, scopulae lacking. *Female palp:* long and slender, terminal claw apparently lacking. *Male palp:* simple; retrolateral tibial apophysis distally blunt or pointed; embolus originating subbasally to apically, shape relatively short and stout to moderately long and slender; tegulum unmodified, seminal duct peripheral. *Epigyne:* relatively simple; openings indistinct; posteriorly a semicircular depression (presumably for retaining the retrolateral tibial apophysis during copulation); primary spermathecae small, secondaries large with leaf-like fertilization ducts.

AFFINITIES AND DIAGNOSIS. The simple structure of the secondary genitalia would appear to exclude this genus from the Lyssomaninae, unfortunately affinities with other salticine subfamilies are unknown and a useful diagnosis cannot be given at the present time. Hopefully the position will become clear when other Oriental genera have been revised.

REMARKS. It may be of interest to note that a survey of Oriental salticids in the collections of the British Museum (Natural History) produced several pale yellow females from the Malay Peninsular which were initially considered to be congeneric with *Orthrus,* but later proved otherwise. Similarly, the New Guinea collections produced several males with elongate chelicerae that closely resembled *Orthrus,* but these too belonged in another 'unknown' and unrelated genus.

List of species in the genus *Orthrus* Simon 1900
Orthrus bicolor Simon, 1900
O. muluensis sp. n.
O. palawanensis sp. n.

An identification key is hardly necessary as the species can be readily distinguished from one another by the structure of the genitalia.

Orthrus bicolor Simon
(Fig. 1A–E)

Orthrus bicolor Simon, 1900 : 28, ♂. LECTOTYPE ♂, PARALECTOTYPE juvenile [not adult ♀] (here designated), Philippines, Antipolo (MNHN, Paris, no. 20560) [Examined]. Simon, 1901 : 394–96, 400. Petrunkevitch, 1928 : 181. Roewer, 1954 : 932. Bonnet, 1958 : 3215..

AFFINITIES AND DIAGNOSIS. *O. bicolor,* seems to be most closely related to *O. palawanenesis* sp. n., but may be distinguished by the form of the chelicerae (Fig. 1A, E) and the blunt retrolateral tibial apophysis (Fig. 1C).

FEMALE. Unknown.

MALE LECTOTYPE. *Carapace* (Fig. 1A, B): orange-brown grading to pale yellow-brown in foveal region and eye area. *Eyes:* with black surrounds except AM; anterior medians on large pedestals, sparsely fringed in fine pale yellowish hairs; anterior row more or less contiguous with apices recurved. *Clypeus:* very sparsely fringed in fine clear hairs. *Chelicerae* (Fig. 1A, E): elongate, divergent from near bases, porrect; pale orange, shiny; lateral keels sparsely fringed in fine yellowish hairs; promargin with 3 teeth, retromargin with 6. *Maxillae:* pale brown to whitish yellow. *Labium:* pale brown edged whitish yellow. *Sternum:* whitish yellow, shiny; margins poorly defined. *Coxae:* pale yellow. *Abdomen:* whitish yellow. *Legs:* light yellowish; spines very pale, spination of legs I: metatarsi V 2-2-0, R 1-0-1, P 1-0-1; tibiae V 2-4-0, R 0-0-1, P 0-1-1; femora apparently D 0-1-0. *Palp* (Fig. 1C, D): femora fringed dorsally and ventrally with stiff orange hairs, patellae and tibiae fringed ventrally with stiff brown hairs.

Dimensions (mm): total length 4·78; carapace length 1·54, breadth 1·26, height 0·92; chelicerae length 0·88; abdomen length 2·44; eyes, anterior row 1·14, middle row 0·9, posterior row 1·0; quadrangle length 0·78. *Ratios:* AM : AL : PM : PL : 12 : 5 : 1·2 : 4·1; AL – PM – PL : 4 – 5·5; AM : CL (clypeus) : 12 : 1, chelicera length/carapace length 0·57.

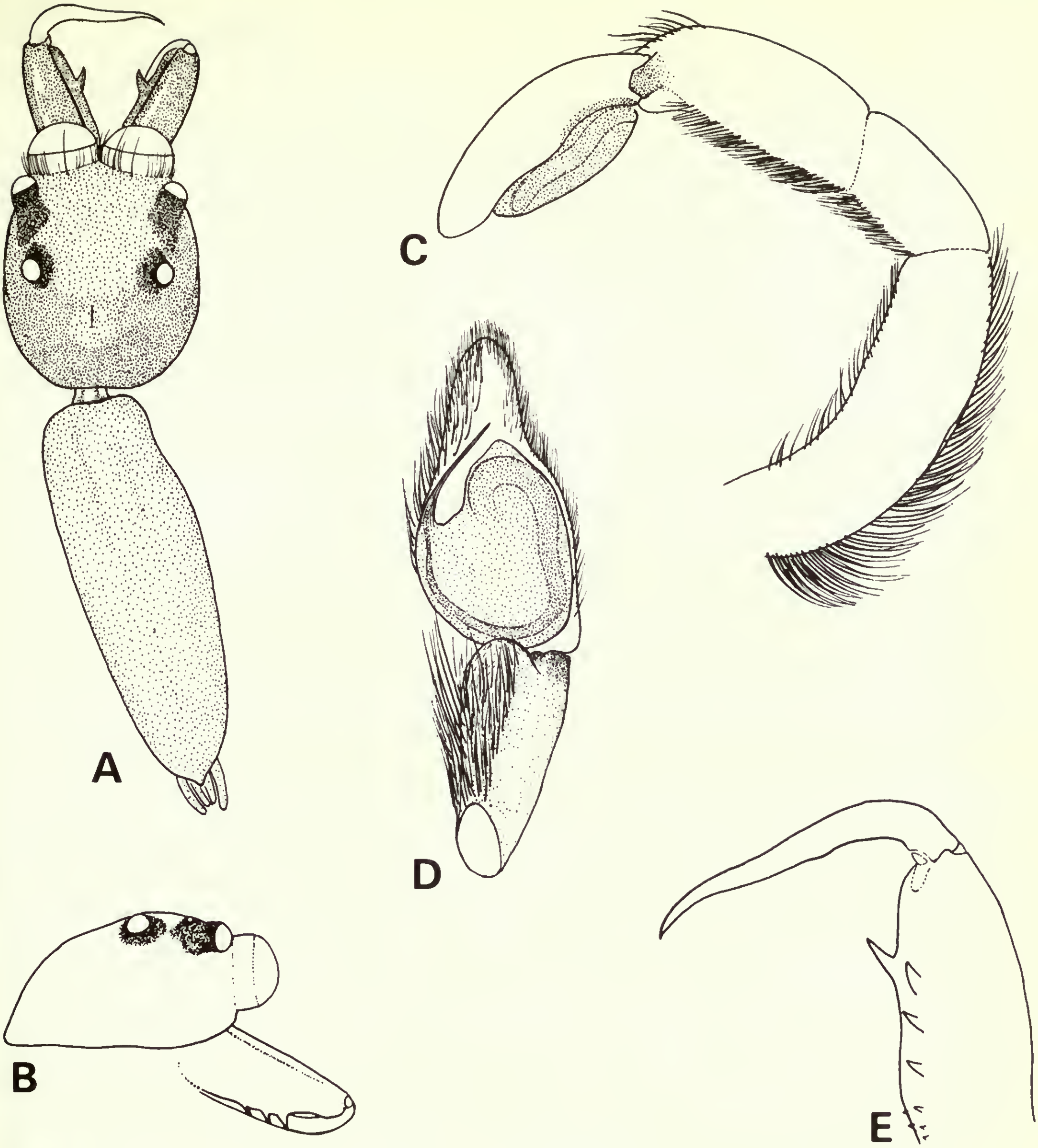

Fig. 1 *Orthrus bicolor* Simon, lectotype ♂: A, dorsal view; B, carapace, lateral view; C, palp, lateral view; D, palp, ventral view; E, chelicera.

Distribution. Philippines (Antipolo, environs of Manila).

Material examined. Lectotype ♂, paralectotype juvenile, data given in synonymy.

Orthrus palawanensis sp. n.
(Fig. 2A–F)

Affinities and diagnosis. *O. palawensis,* is apparently closest to *O. bicolor,* but may be readily separated by the form of the chelicerae (Fig. 2A, F) and the curved retro-lateral tibial apophysis (Fig.2C).

Female. Unknown.

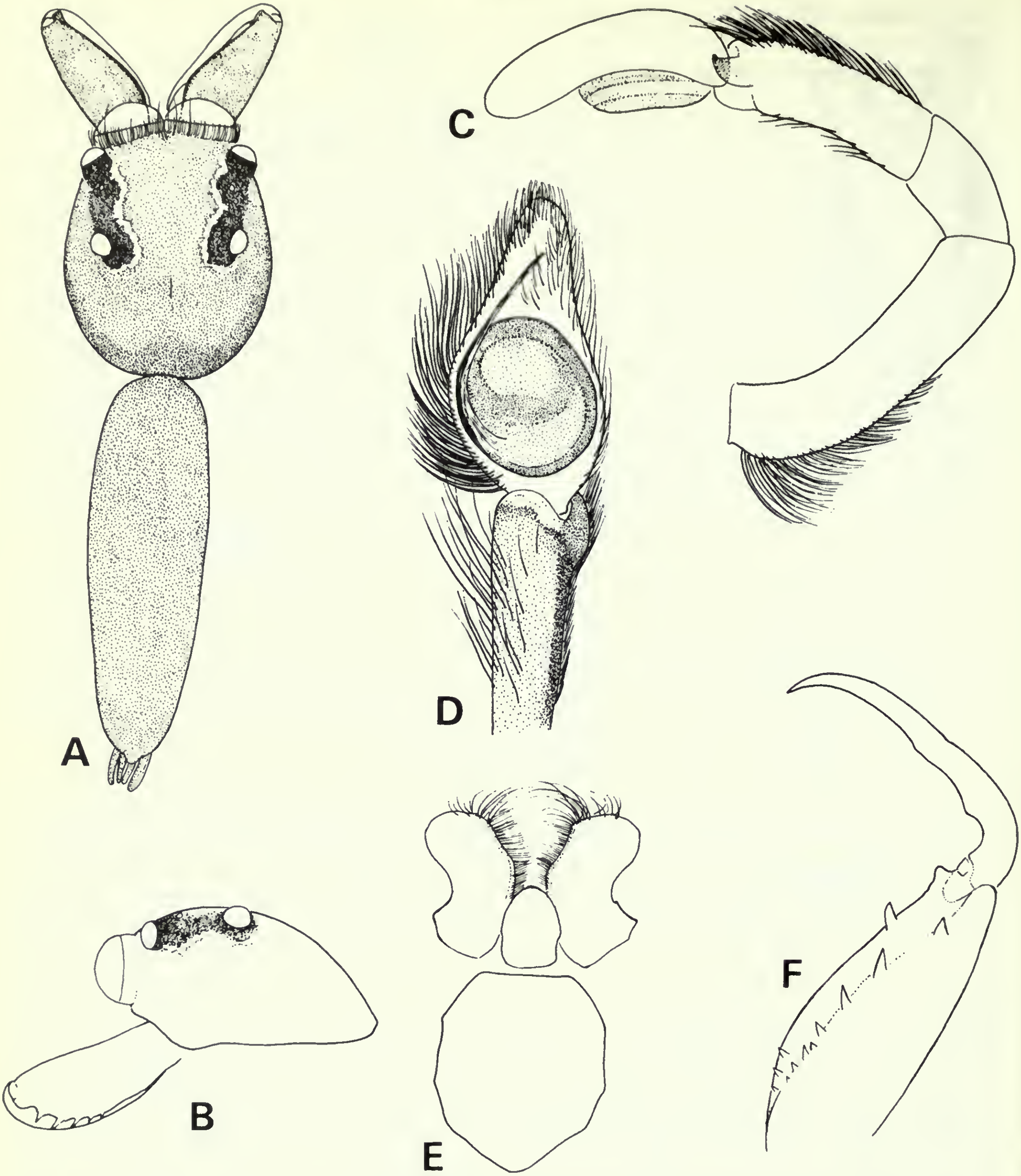

Fig. 2 *Orthrus palawanensis* sp. n., holotype ♂: A, dorsal view; B, carapace, lateral view; C, palp, lateral view; D, palp, ventral view; E, maxillae, labium and sternum; F, chelicera.

MALE HOLOTYPE. *Carapace* (Fig. 2A, B): pale orange-brown with sooty margins; shiny. *Eyes:* with black surrounds edged in yellowish guanin, except AM; fringed in whitish hairs; anterior row more or less contiguous with apices recurved. *Clypeus:* orange-brown lightly tinged black. *Chelicerae* (Fig. 2A, F): elongate, strongly divergent from just before mid-length, porrect; amber; shiny; promargin with 4 teeth, retromargin with 7 or 8. *Maxillae* (Fig. 2E): pale yellow lightly tinged grey. *Labium:* pale yellow. *Sternum* (Fig. 2E): pale yellow, shiny. *Abdomen:* pale yellow; spinnerets moderately elongate, pale yellow very lightly tinged black. Coxae: pale yellow. *Legs:* legs I pale yellow with blackish lateral stripes on tarsi, metatarsi, tibiae and patellae, also with dorsal and ventral fringes of grey-black lanceolate hairs on tibiae, patellae and proximal part of metatarsi; other legs pale yellow with greyish black longitudinal lateral stripes on tarsi and metatarsi, fringes lacking; spinnation of legs I: metatarsi V 2-2-0, R 1-0-1, P 1-0-1; tibiae V 2-4-2-, R 1-1-0, P 1-1-0; patellae V 0-1-0; femora R 0-0-1, D 1-1-1, P 0-0-1. *Palp* (Fig. 2C, D): yellow-orange with grey-black lateral stripes; femora and tibia with dorsal fringe of blackish hairs.

Dimensions (mm): total length 4·1; carapace length 1·66, breadth 1·42, height 0·96; chelicerae length 0·92; abdomen length 2·44; eyes, anterior row 1·2, middle row 0·98, posterior row 1·14; quadrangle length 0·86. *Ratios:* AM : AL : PM : PL : 12 : 5 : 1 : 5; AL – PM – PL : 4 – 6·5; AM : CL : 12 : 1; chelicera length/carapace length 0·65.

VARIATION. A paratype ♂ measures 4·5 m total length, 1·88 mm carapace length, 1·28 mm cheliceral length; ratio of chelicera/carapace length 0·68. This specimen is generally paler than the holotype and the lateral stripes on the legs and palps are lacking.

DISTRIBUTION. Philippines.

MATERIAL EXAMINED. PHILIPPINES: Palawan, Mantalingajan, Tagembung, 1150 m, (*Noona Dan Exp.,* 1961–62) holotype ♂, 20.ix.1961 (ZM, Copenhagen) paratype ♂, 17.ix.1961 (BMNH. 1979.5.14.1).

Orthrus muluensis sp. n.

(Figs. 3A–G; 4A–D)

AFFINITIES AND DIAGNOSIS· *O. muluensis* is closely related to *O. bicolor* Simon and *O. palawanensis* sp. n., but can be distinguished by the absence of fringes on the male palp (Fig. 3C), and distribution.

MALE HOLOTYPE. *Carapace* (Fig. 3A, B): pale yellow grading to light brown in eye region with median and marginal brown-black bands; pale areas clothed in recumbent silky white hairs. *Eyes:* with black surrounds edged in whitish yellow guanin, except AM; fringed in silky white hairs; anterior row more or less contiguous with apices recurved. *Clypeus:* black. *Chelicerae* (Fig. 3A, F, G): elongate and porrect; brown-black, shiny; promargin with 3 teeth, retromargin with 6. *Maxillae:* brown-black with inner and distal margins pale yellow. *Labium:* brown-black to pale yellow. *Sternum:* pale yellow, shiny. *Coxae:* pale yellow, but coxae I with black lateral sides. *Abdomen:* brown-black with pale yellow longitudinal bands; thinly clothed in fine light yellow hairs; spinnerets moderately elongate; brown-black. *Legs:* legs I pale yellow with black lateral stripes on metatarsi, tibiae, patellae and trochanters; also a fringe of short stiff black hairs on venter of tibiae; other legs pale yellow with grey-black apices on tibiae IV; spination of legs I: metatarsi V 2-2-0, R 1-0-1, P 1-0-1; tibiae V 2-4-0, R 0-0-1, P 0-0-1; femora D 1-1-2, P 0-0-1. *Palp* (Fig. 3C, D): whitish yellow with black retrolateral stripes on coxae and femora; fringes lacking.

Dimensions (mm): total length 4·0; carapace length 1·52, breadth 1·24, height 0·10; chelicerae length 1·44; abdomen length 2·4; eyes, anterior row 1·12, middle row 0·88, posterior row 0·98; quadrangle length 0·8. *Ratios:* AM : AL : PM : PL : 11 : 5 : 1·2 : 4·7; AL – PM – PL : 5 – 5; AM : CL : 11 : 1; chelicerae length/carapace length 0·95.

FEMALE PARATYPE. *Carapace* (Fig. 4A): pale yellow to whitish yellow in eye region. *Eyes:* with black surrounds edged in whitish guanin, except AM; fringed in silky white hairs. *Clypeus:* pale yellow. *Chelicerae:* pale yellow, shiny; promargin with 3 teeth, retromargin with 7. *Maxillae and labium:* pale yellow. *Sternum:* whitish yellow. *Abdomen:* pale yellow with a whitish spot just in front of the anal tubercle; spinnerets moderately elongate. *Legs:* pale yellow; spination of legs I: metatarsi V 2-2-0, R 1-0-1, P 1-0-1, tibiae V 2-4-2, R 0-1-0, P 0-1-0; patellae V 0-1-0; femora D 1-1-1, P 0-0-1. *Palp:* pale yellow. *Epigyne* (Fig. 4B–D): small and pale; openings indistinct.

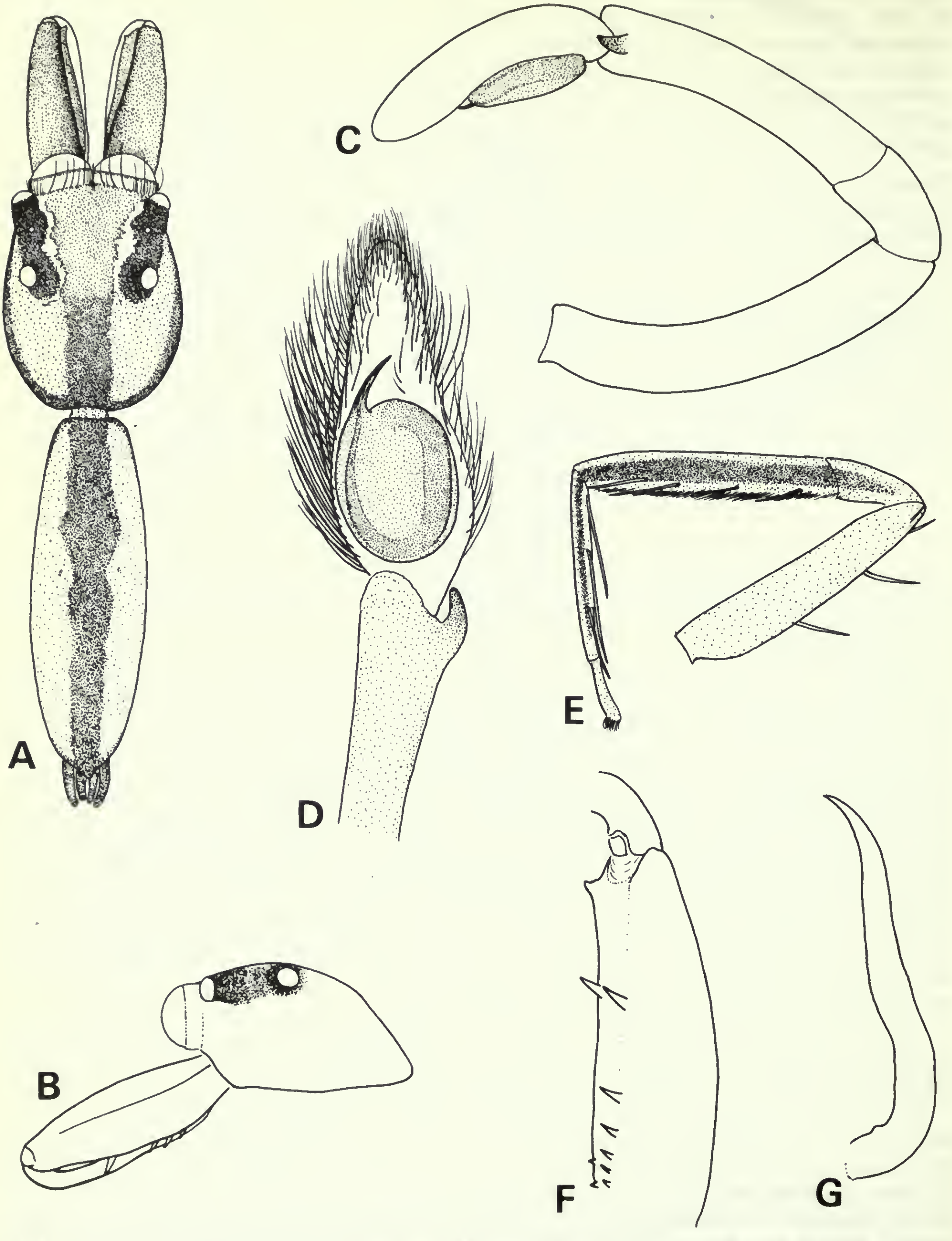

Fig. 3 *Orthrus muluensis* sp. n., holotype ♂: A, dorsal view; B, carapace, lateral view; C, palp, lateral view; D, palp, ventral view; E, leg I; F, chelicera; G, fang.

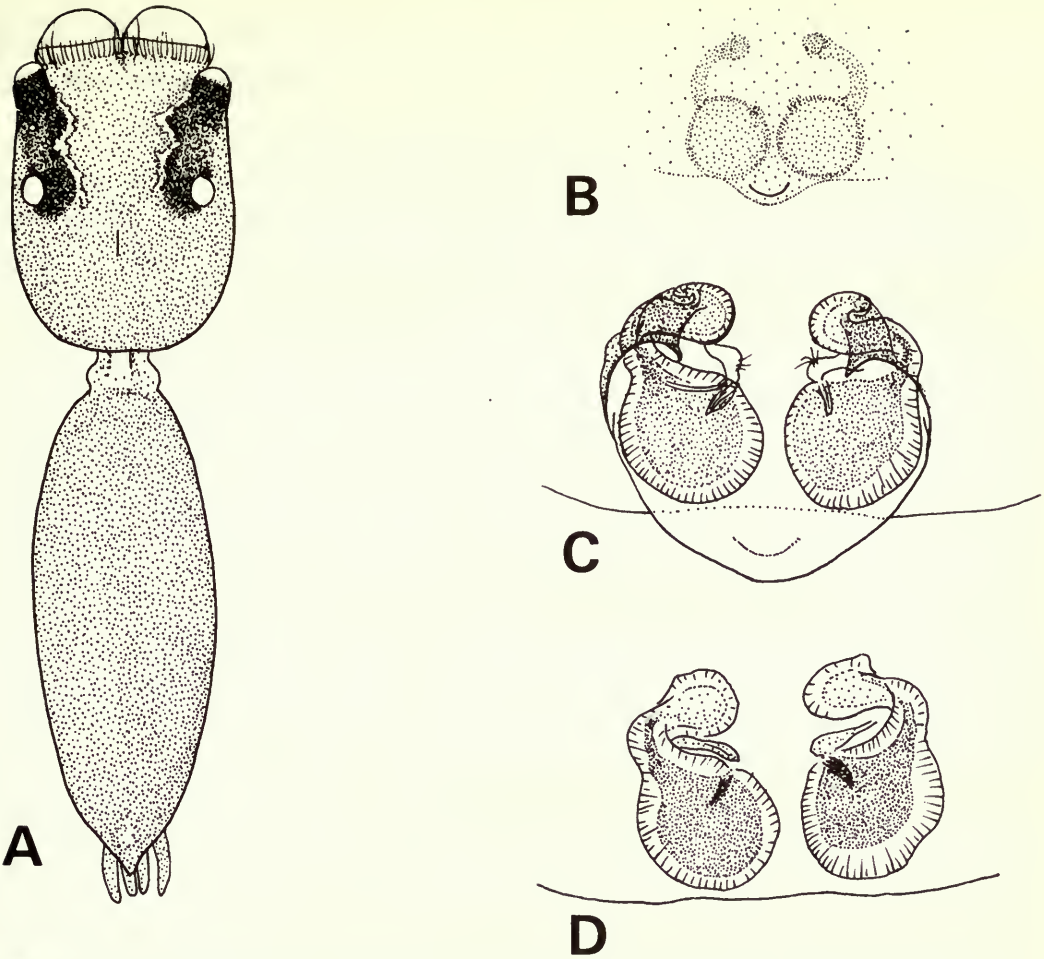

Fig. 4 *Orthrus muluensis* sp. n., paratype ♀: A, dorsal view; B, epigyne; C, vulva, ventral view; D, vulva, dorsal view.

Dimensions (mm): total length 3·88; carapace length 1·44; breadth 1·13, height 0·76; abdomen length 2·24; eyes, anterior row 1·08, middle row 0·82, posterior row 0·96; quadrangle length 0·71. *Ratios:* AM : AL : PM : PL : 10 : 4·5 : 1 : 4·1; AL – PM – PL : 4·5 – 5; AM : CL : 10 : 2.

Variation. Males 4·2 to 4·8 mm total length, 1·54–1·66 mm carapace length; cheliceral to carapace length varies from 0·95–1·06 (3 specimens); another paratype female measures 3·92 mm in total length, 1·52 mm carapace length.

Biology. Females and juveniles are green in life and were collected from the underside of green leaves on shrubs and young trees in alluvial forest. One female was found under a leaf guarding a parchment-covered group of ten light green eggs measuring approximately 0·68 mm diameter. She appeared to be resting upside down, beneath a flimsy web spun just above the cocoon which was camouflaged with particles of detritus. Males were found running about on ginger leaves. The sexes were not taken together, but occurred in the same locality. This species, which was not often encountered, in spite of diligent searching, is possibly more abundant in the canopy.

Distribution. Sarawak.

Material examined. SARAWAK, Gunong Mulu National Park (*F. R. Wanless* Royal

Geographical Society Mulu exp., 1977–78): Gua Payau, cave entrance, under ginger leaves, holotype ♂, paratype ♂, 16.vi.1978 (BMNH. 1979.5.18.1–2); Environs of Melinau Gorge, under leaves, 29–30.vi.1978, paratypes, 1♀ (BMNH), 1♂, 1♀ (Sarawak Museum, Kuching).

Acknowledgements

I wish to thank the following colleagues for providing specimens for study. M. M. Hubert, Muséum national d'Histoire naturelle, Paris, France (MNHN, Paris) and Dr. Borge Petersen, Zoological Museum, Copenhagen, Denmark (ZM, Copenhagen).

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A note on *Lonchophylla* (Chiroptera: Phyllostomatidae) from Ecuador and Peru, with the description of a new species

J. E. Hill

Department of Zoology, British Museum (Natural History) Cromwell Road, London SW7 5BD

Introduction

The glossophagine genus *Lonchophylla* extends from Nicaragua to Peru, Bolivia, Brazil and Surinam. Of the six species currently recognised (Jones & Carter, 1976 : 15; Sazima, Vizotto & Taddei, 1978 : 81) *L. concava, L. robusta* and *L. thomasi* are comparatively widespread: another, *L. hesperia,* has been reported only from Peru, and the recently described *L. bokermanni* Sazima, Vizotto & Taddei, 1978 is known solely from the type locality in Minas Gerais, Brazil. Only *L. mordax* has been recorded from Ecuador, by Baker (1974 : 136), at a location 45 km NE of Chone (00°41′S, 80°05′W) in Manabi Province in the northwestern coastal belt, but occurs also in Bolivia and Brazil.

Specimens of *Lonchophylla* were obtained in 1976 by Mr. A. M. Hutson of the Department of Entomology, British Museum (Natural History), London and Mr. R. E. Stebbings of the Institute of Terrestrial Ecology, Monks Wood Experimental Station, Abbots Ripton, Huntingdon, England, while collecting at Yaupi and Los Tayos, Morona Santiago Province, in southeastern Ecuador near the border with Peru. Some represent *L. robusta* but others cannot be assigned to any of the described species: specimens similar to these have been reported (as *L. robusta*) from Peru.

Specimens examined or discussed are in the British Museum (Natural History) (BM(NH)), London; the United States National Museum of Natural History (USNM), Smithsonian Institution, Washington; the American Museum of Natural History (AMNH), New York, and the Texas Wildlife Cooperative Research Collection (TCWC), Texas A & M University, College Station, Texas.

Lonchophylla robusta Miller, 1912

Material examined. ECUADOR: Yaupi, Morona Santiago Province, 02°93′S, 77°54′W. ♀♀ BM(NH) 78.1354–1355, 78.1358–1362, sex unknown 78.1356–1357 (all in alcohol, skulls extracted). 30 July 1976.

Remarks. Although not hitherto recorded from Ecuador, *Lonchophylla robusta* is known to occur in Costa Rica, Panama, Venezuela and Colombia (Jones & Carter, 1976 : 16; Sazima, Vizotto & Taddei, 1978 : 81). Specimens from Yaupi agree closely with the diagnosis and description by Miller (1912 : 23) and are similar in size (Table 1) to those from Costa Rica and Panama reported by Walton (1963 : 88) or from Venezuela by Linares (1967 : 60).

Lonchophylla handleyi sp. nov.

Holotype. BM(NH) 78.1368. Adult ♀ (in alcohol, skull extracted). Los Tayos, Morona Santiago Province, Ecuador, 03°07′S, 78°12′W. 14 July 1976. Collector's Number 36.

Other material examined. ECUADOR: Los Tayos. ♂♂ BM(NH) 78.1364, 78.1366, 78.1369–1370, 78.1372, ♀♀ 78.1363, 78.1367, 78.1371 (all in alcohol, skulls extracted), 78.1373 (in alcohol), 78.1374–1376 (all in alcohol, skulls extracted). 10–26 July 1976. ♂

Bull. Br. Mus. nat. Hist. (Zool.) **38** (4): 233–236 Issued 25 September 1980

Table 1 Measurements (in millimetres) of *Lonchophylla robusta* and *L. handleyi*

	L. robusta Ecuador			*L. handleyi* Ecuador							
	Number of specimens	Range	Mean	Number of specimens	Range	Mean	Holotype ♀ BM(NH) 78.1368 Los Tayos, Ecuador	♀ USNM 364347 Peru	♂ USNM 507172 Peru	♂ AMNH 230214* Peru	♀ TCWC 11879** Peru
Length of forearm	9	42·3–45·5	(43·3)	18	44·4–47·9	(46·1)	45·6	46·1	47·0	44·7	45·1
Length of tibia	9	16·0–17·5	(16·8)	18	17·0–18·5	(18·0)	17·5	18·3	17·8	15·4	15·6
Width of interfemoral membrane at centre	9	12·3–14·3	(13·4)	18	8·0–11·4	(9·3)	10·0	8·6	9·2	5·9	7·0
Greatest length of skull	9	25·3–26·2	(25·9)	16	27·5–29·2	(28·5)	28·5	27·4	27·4	26·9	27·5
Condylobasal length	9	23·7–24·6	(24·2)	16	26·3–28·1	(27·2)	27·2	26·2	26·5	25·9	25·4
Condylocanine length	9	23·0–23·9	(23·5)	16	25·5–27·2	(26·4)	26·3	25·3	25·5	25·0	24·8
Basal length	9	21·7–22·6	(22·2)	16	24·0–25·6	(25·0)	24·7	23·8	23·9	23·3	23·4
Palatal length	9	13·6–14·4	(13·9)	15	16·1–17·5	(16·8)	16·8	15·9	16·0	15·4	15·4
Length of bony palate (m^3–m^3 to palation)	9	3·5–3·9	(3·7)	16	5·0–5·5	(5·3)	5·4	5·1	5·1	4·4	5·0
Length of mesopterygoid canal (palation to tips of hamulars)	7	3·7–4·1	(3·9)	16	3·2–4·1	(3·8)	3·9	3·9	4·0	3·9	3·9
Width of rostrum above canine roots	9	3·7–4·1	(3·9)	16	4·2–4·4	(4·3)	4·2	4·2	4·2	3·9	4·2
Width of rostrum across anteorbital foramina	9	4·2–4·7	(4·4)	16	4·7–5·0	(4·9)	4·8	4·8	4·9	4·5	4·9
Least interorbital width	9	4·7–5·2	(4·9)	16	4·9–5·2	(5·0)	4·9	5·2	5·2	4·6	5·0
Least postorbital width	9	5·0–5·3	(5·1)	16	5·1–5·5	(5·3)	5·2	5·3	5·1	5·0	5·3
Width of braincase	9	9·7–10·1	(9·9)	16	10·0–10·5	(10·2)	10·3	10·4	10·1	9·7	10·5
Mastoid width	9	10·2–10·8	(10·5)	16	10·9–12·0	(11·4)	11·6	11·4	11·3	10·6	11·0
c^1–c^1 (crowns)	9	4·0–4·4	(4·2)	16	4·5–4·9	(4·7)	4·6	4·5	4·7	4·2	4·5
m^2–m^2 (alveoli)	9	6·1–6·5	(6·3)	16	6·6–7·0	(6·8)	6·7	6·7	6·7	6·1	6·1
Width of mesopterygoid fossa	9	1·9–2·1	(2·0)	16	1·8–2·2	(2·0)	2·0	2·0	1·8	1·4	2·1
c–m^3	9	9·1–9·6	(9·4)	16	10·2–11·0	(10·6)	10·4	10·1	10·1	10·0	10·0
Length complete mandible from condyles	8	17·0–17·6	(17·3)	14	19·1–20·3	(19·8)	19·8	19·2	19·0	—	18·5
Length of right ramus from condyle	9	17·5–18·2	(17·9)	14	19·6–21·0	(20·3)	20·3	19·8	19·5	19·2	18·8
c–m_3	9	9·5–10·0	(9·8)	16	10·5–11·4	(10·9)	10·7	10·4	10·4	10·3	10·3

* *measured by Dr. K. F. Koopman* ** *measured by Professor W. B. Davis*

Collector's Number 35 (in alcohol), ♀ 11 (in alcohol, skull extracted). Yaupi, Morona Santiago Province, 02°93′S, 77°54′W. ♂ BM(NH) 78.1377, ♀ 78.1378 (both in alcohol, skulls extracted). 30 July 1976. PERU: San Juan, Oxapampa Province, Pasco Department, 900 ft, 10°30′S, 74°53′W. ♀ USNM 364347 (skin and skull). 5 August 1964. 3·2 km N of Vitoc, Rio Tulamayo, Tarma Province, Junin Department, 700 m, c. 11°10′S, 75°15′W. ♂ USNM 507172 (skin and skull). 16 November 1974.

OTHER MATERIAL DISCUSSED. PERU: 3 km NW of San Ramón, Tarma Province, Junin Department, 2900 ft, 11°08′S, 75°22′W. ♂ AMNH 230214 (skin and skull). 28 June 1964. 3 mi S of Tingo Maria, Huanucu Province, Huanucu Department, 2400 ft, c. 09°09′S, 75°56′W. ♀ TCWC 11879 (skin and skull). 28 August 1964.

DIAGNOSIS. Readily distinguished from *Lonchophylla hesperia, L. mordax, L. concava, L. thomasi* and *L. bokermanni* by greater size; similar in most respects to *L. robusta* but generally larger (Table 1); interfemoral membrane or uropatagium narrower, with a sparse fringe of short hairs along much of its posterior margin; bony post-palate absolutely and relatively longer, its lateral margins more flange-like and its palatal face more deeply excavated, the median palatal furrow extending further posteriorly almost to the anterior edge of the mesopterygoid fossa; internal basal cusp of second upper premolar (pm^4) less developed.

DESCRIPTION. Largest (length of forearm 44·4–47·9 mm, greatest length of skull 26·9–29·2 mm) of the genus *Lonchophylla* as currently known; muzzle elongate; noseleaf low, broadly based, its lateral margins faintly concave; ears large, broad and rounded as in *L. robusta*; tragus spatulate, its length about one third the length of the ear; tail short or very short, usually as in *L. robusta* just emerging from the dorsal surface of the interfemoral membrane about halfway across its width but sometimes barely perceptible; interfemoral membrane narrow, the more central part of its posterior margin edged with a sparse fringe of short hairs; wings inserted at the ankle; calcar short, cartilaginous.

Skull generally similar to that of *L. robusta*; rostrum long and broad, especially anteriorly at the canine alveoli; braincase full, rounded; bony post-palate long, its lateral margins projecting slightly as a narrow flange; V-shaped median longitudinal palatal furrow extending posteriorly almost to the mesopterygoid fossa so that the post-palatal extension is centrally grooved for much of its length, in contrast to the flatter, less deeply excavated post-palate of *L. robusta*; mesopterygoid canal relatively short; coronoid process high and prominent.

Dentition normal for the genus, the teeth generally a little more massive than those of *L. robusta,* but with the upper premolars (pm^{3-4}) and the first and second lower premolars (pm_{2-3}) about the same size as in that species; postero-internal basal cusp of pm^4 small and undeveloped, occasionally very small and insignificant; first and second upper molars with long inner margin, their crowns subsquare, lower molars with broad crowns; lower incisors faintly trilobate.

REMARKS. Tuttle (1970 : 68) tentatively allocated two specimens (USNM 364347, AMNH 230214) from Peru to *Lonchophylla robusta,* observing that they were larger than typical examples of this species and had a narrow interfemoral membrane with a sparse but distinct fringe of short hairs along its posterior edge. Subsequently, Gardner (1976 : 5) referred a third Peruvian example (USNM 507172) to *L. robusta* and remarked that it compared favourably with most of the characters outlined by Tuttle for his material. These specimens are the basis of the brief discussion of records of *L. robusta* from Peru by Koopman (1978 : 6). Two (USNM 364347, USNM 507172) have been examined and clearly represent *L. handleyi.* The measurements (Table 1) of the third (AMNH 230214) and of an unrecorded Peruvian example (TCWC 11879) of *Lonchophylla* refer these also to this species, although the bony palate of AMNH 230214 is rather shorter than is usual in *L. handleyi.* The skulls of the Peruvian examples of *L. handleyi* so far available are generally a little shorter than are those of specimens from Ecuador.

The two specimens (USNM 364347, USNM 507172) from Peru that have been examined are the only examples seen that have not been preserved in alcohol. Dorsally, both are light brown, with a faint red tinge, the hairs on the head, shoulders and anterior back whitish or slightly creamy at the base and for much of their length, heavily tipped with brown, the pale colour showing clearly on the sides of the throat and on the shoulders. On the lower back the pelage is more nearly unicolorous, the hairs brown for most of their length and pale only at the base. The ventral surface is buffy brown, the hairs on the chin, throat and on the anterior part of the chest unicolorous but posteriorly the hairs are browner at the base with heavy buffy brown tips. There is a sprinkling of brown hairs on both surfaces of the interfemoral membrane: the short, sparse hairs fringing its posterior margin are whitish, in USNM 364347 extending along the edge about halfway to the legs although slightly denser medianly, but USNM 507172 has a more than usually sparse fringe, its few very short hairs concentrated at and near the centre of the edge of the membrane. This specimen has also a very short and inconspicuous tail.

ETYMOLOGY. This new species has been named after Dr C. O. Handley, Curator of Mammals at the United States National Museum of Natural History, Smithsonian Institution, Washington. Dr Handley generously placed his notes on the large specimens of Peruvian *Lonchophylla* at my disposal, together with a number of measurements, having recognised some years ago that a new species might be involved.

Acknowledgements

My thanks are due to Dr A. L. Gardner of the National Fish and Wildlife Laboratory at the United States National Museum of Natural History, Smithsonian Institution, Washington, who made possible a direct examination of certain Peruvian specimens of *Lonchophylla* from that collection; to Dr Karl F. Koopman of the Department of Mammalogy, American Museum of Natural History, New York, for providing measurements of a further Peruvian specimen in his care and for directing my attention to certain of the relevant literature; and to Dr D. C. Carter of the Graduate School and Office of Academic Publications, Texas Tech University, Lubbock and to Professor W. B. Davis and Dr J. W. Bickham of the Department of Wildlife and Fisheries Sciences, Texas A & M University, College Station, Texas, who provided measurements of a specimen of *Lonchophylla* from Peru in the Texas Cooperative Wildlife Research Collection. I have also to record the generous action of Mr G. L. Graham of the Museum of Natural Science, Louisiana State University, Baton Rouge, in relinquishing an interest in the large *Lonchophylla* of Peru on learning of the present study.

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Bulletin of the British Museum (Natural History)

Mites of the subfamily Parasitinae (Mesostigmata: Parasitidae) in the British Isles

Keith H. Hyatt

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Mites of the subfamily Parasitinae (Mesostigmata: Parasitidae) in the British Isles

Keith H. Hyatt K

Department of Zoology, British Museum (Natural History), Cromwell Road, London, SW7 5BD

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Synopsis

The mites of the subfamily Parasitinae in the British Isles and the Channel Islands are revised. Thirty-six species belonging to nine genera are recorded of which one is new to science and fourteen are new to the British fauna. Habitat and distributional data are given and keys to the genera and species for deutonymphs, males and females are provided. The taxonomy includes eleven new specific synonyms and five new combinations.

Introduction

The Parasitidae are among the most common and widely distributed mites of the suborder Gamasina to be found in litter and humus, and certain species are especially abundant in accumulations of organic material such as rotting seaweed, compost, dung and in the subterranean nests of small mammals. Others are associated with bumblebees and burying-beetles during part of their life-cycle (the *nympha coleoptrata* stage), the 'host' being used as a

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means of transport. They are essentially predatory and feed upon other microarthropods, including their eggs, and on nematodes, and are rivalled in size and abundance by two other gamasine families, the Macrochelidae and the Veigaiidae.

With the exception of the work by Bhattacharyya (1963) on *Pergamasus* s. lat., there has been no revision of the remaining genera and species of British Parasitidae since that of Hull (1918), although additional species records and changes in nomenclature are documented by Turk (1944, 1945, 1953) and Turk & Turk (1952) – a quarter of a century ago. It is appropriate to mention here the unpublished thesis of Colombo (1961) in which valuable contributions are made on the developmental stages of those species associated with bees of the genus *Bombus*. On the continent of Europe, however, we have the works of Schweizer (1961) and Karg (1971), in which revisions are made for Switzerland and Germany respectively, whilst Micherdzinski (1969) has attempted a revision of the entire family based on fresh material from Poland, Germany, Czechoslovakia, China and Kashmir, together with a detailed study of past literature. More recently Bregetova *et al.* (1977) have produced a large work on the soil-inhabiting Mesostigmata. Their coverage, however, is more in the order of an amalgamation of keys from existing works.

The classification followed in the present work is that proposed by Evans and Till (1979) in which nine genera are recognized.

During the preparation of the present work the opportunity has been taken, where possible, to check on the identity of material constituting earlier British records. Also, as far as possible, papers recording the occurrence of parasitines in the British Isles have been referred to, although it is certain that some, especially general ecological and invertebrate papers, have been missed. Indeed, I should be pleased to learn of such records and to receive material to confirm identifications. The record of *Parasitus neglectus* (Berlese, 1904*a*) by Turk & Turk (1952) has not been verified as the specimen cannot at present be found (Dr F. A. Turk *in litt.*). Similarly with the senior author's citation (Turk, 1953) of *P. hortivagus* (Berlese, 1904*a*). *Parasitus wasmanni* Oudemans, 1902*b*, also recorded by Turk (1953), has been transferred to *Pergamasus* (Bhattacharyya, 1963, Micherdzinski, 1969, Karg, 1971).

The records quoted for distribution abroad are assumed to be referable to the species in question, but where they have already been diagnosed as otherwise this is noted. Also, the overseas distribution given for each species is not claimed to be complete as papers of an applied nature are not always widely circulated.

Material

This revision is based on the examination of over ten thousand specimens from the following sources:

(*a*) The named material already curated into the collections of the British Museum (Natural History), some of it being specimens identified by A. S. Hirst during the first quarter of this century.

(*b*) Approximately one thousand Berlese-funnel extractions (from a total of just over two thousand) collected mainly in recent years and housed in the Arachnida Section, BM(NH).

(*c*) A large part of the collections of the late Harry Britten senior, deposited partly in Manchester Museum and partly in the BM(NH), the latter forming part of the J. H. Murgatroyd collection, and Murgatroyd's own collection containing much useful material.

(*d*) A portion of the collections of the late Rev. J. E. Hull now deposited in the BM(NH).

(*e*) A considerable number of samples or individual specimens from freeliving habitats or associated with beetles and bumblebees, sent to the Museum by naturalists, ecologists, students, or members of the public.

The map, figure 1, shows to the nearest 10-kilometre square on the National and Irish Grids the extent of Berlese-funnel and other samples examined. It follows, therefore, that the blank areas are ones from which no collections have been examined, and not that mites are absent. The map does not show, however, the fact that one square may have been sampled

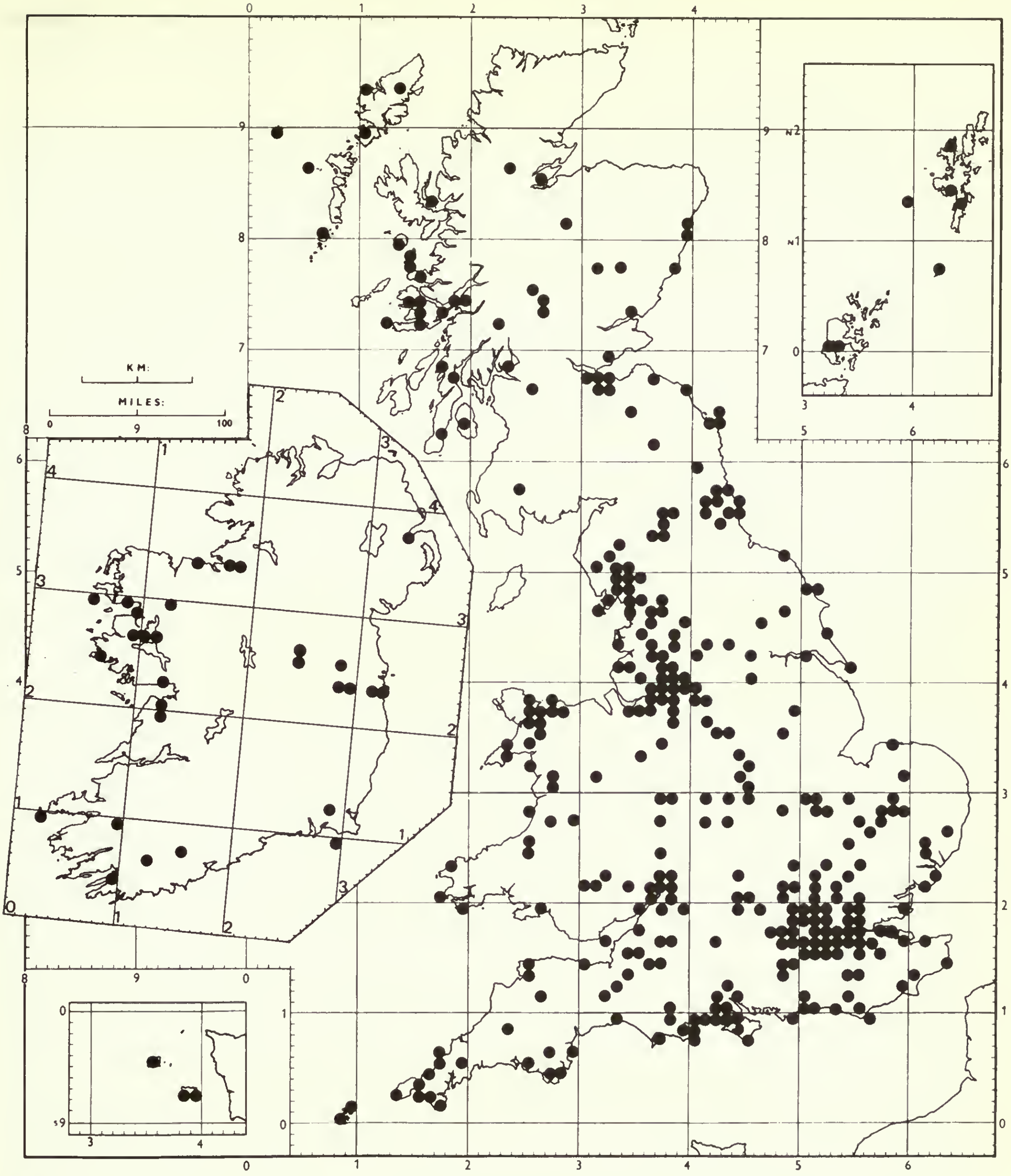


Fig. 1 The National and Irish Grids, showing to the nearest 10-kilometre square the extent of material examined during the preparation of the present work.

extensively, whilst another may be merely the result of a single specimen being collected from a very small sample or even from an individual 'host'. A handful of specimens bearing imprecise locality data have been examined. These are not shown on the map as in each case the county or general area of collection is already dotted. In keeping with most modern British biological recording schemes, the Channel Islands are included, although very few collections have been received from this area.

Consequently the overall distribution of individual species within the British Isles, and especially in Ireland, cannot at this stage be given, although their occurrence within the total area sampled may indicate some trends and relative abundance. As Blower (1974) has concluded for the British millipedes, the incomplete coverage of the country so far makes it premature to discuss reasons for apparent patterns of distribution, although some comments are made under individual species.

Localities are given mainly under the 'old' established counties as this is in keeping with the published reviews of most groups, both plant and animal. Additionally, large urban areas, e.g. Manchester and London, and islands or individual but prominent localities, e.g. Isle of Wight, Lundy, Dungeness and Helvellyn, are given as such. For the scarcer species only, full data are given for each sample. The vast majority of the specimens are curated into the National Collection.

It is intended to continue to accumulate data on British material with a view to updating the distribution and habitat preferences using the present work as a foundation. Therefore fresh material will be gladly received, but even more valuable would be any attempts to rear in the laboratory the complete life-cycles of individual species (for instance *Parasitus magnus* and *berlesei* and *Poecilochirus subterraneus*) as has been done for *Parasitus copridis* (see Costa, 1964).

The principal habitats from which the species documented in this work have been recorded are set out in table 1.

Of the thirty-six species recorded, thirty-five are from Britain and twenty-six are from Ireland. *Trachygamasus gracilis* (Karg) has so far been recorded only in Counties Meath and Kildare, but no significance can be attached to this fact (see also comments on p. 363).

Methods

All material not already permanently mounted on slides has been cleared and examined as temporary slide-mounts in lactic acid, either on being transferred direct from alcohol or, in a few cases, from being preserved dry. Measurements and figures are based on the natural non-compressed curvature of, for instance, the dorsal shields (unless stated otherwise), but measurements of setae are only given of a flat and straight aspect. Details of ornamentation and structure are compared with subsequent specimens and where variations are noted these are, if considered of importance, figured separately. Where many specimens are contained within a single sample (as for instance in *Poecilochirus carabi*) a selection of apparent size and colour forms are cleared and checked for possible significant variation. With little practice a few species can be recognized in alcohol under low magnification as certain degrees of sclerotization and colour tones are more apparent before clearing, e.g. the sternal region of deutonymphs of *Parasitus consanguineus* and *fimetorum* and *Parasitellus fucorum*. Also the difference in the dorsal chaetotaxy between *Parasitus coleoptratorum* and *copridis* is readily seen.

With few exceptions all the figures have been made by camera lucida. The exceptions are when certain developmental stages have not been found in this country, and in these instances the figures are based on those of other authors and are acknowledged accordingly.

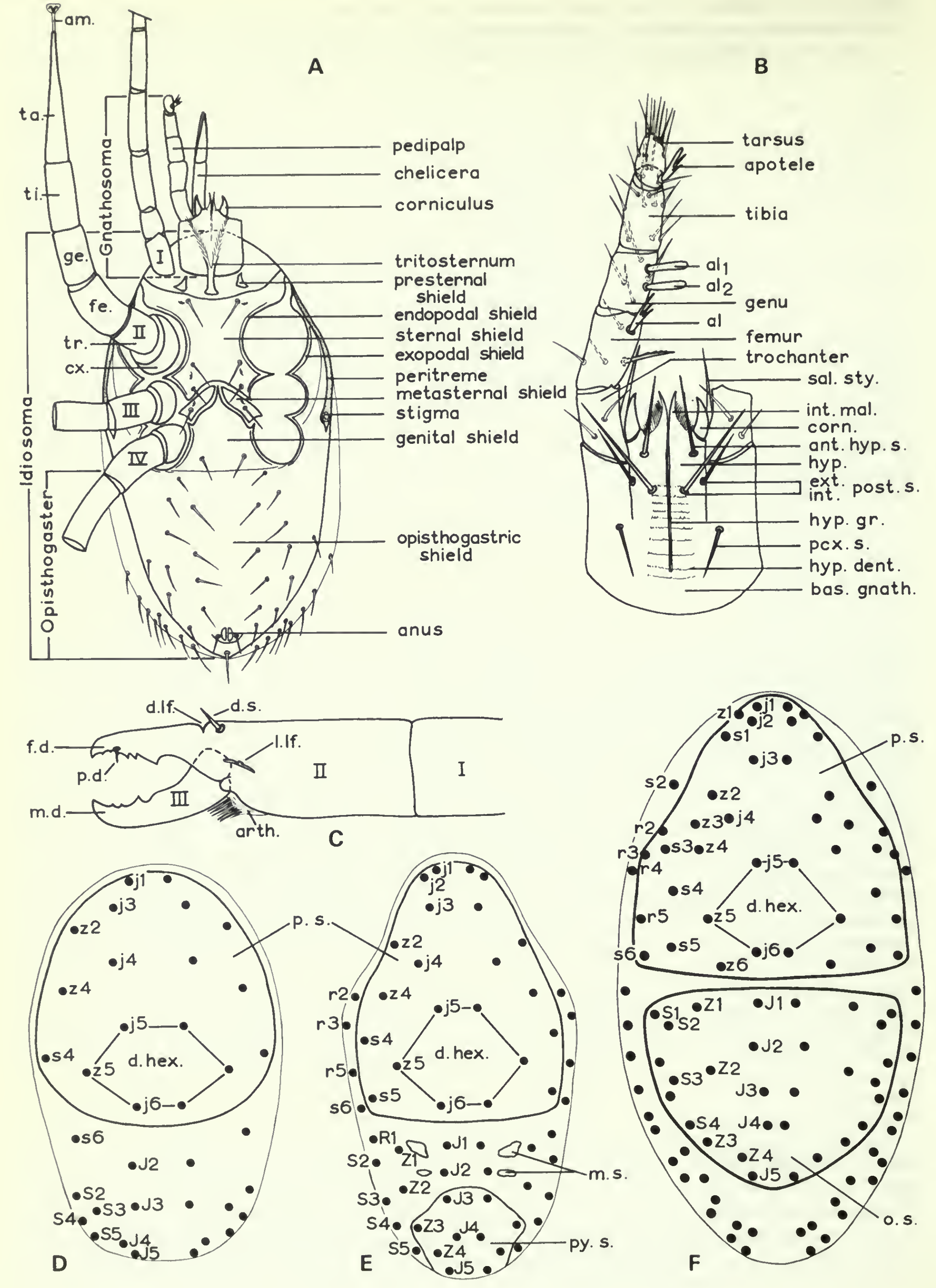
External morphology

The external morphology of the Parasitidae is described at length by Micherdzinski (1969), whilst Bhattacharyya (1963) has discussed that of *Pergamasus* s. lat. However, the terminology used to describe the external morphology of the Acari has been subject to considerable variation, and in the Mesostigmata this has been most pronounced in the gnathosoma. The present simplified account largely follows that of Evans and Till (1979) who base their treatment for the gnathosoma on the freeliving members of the suborder Gamasina, which includes the Parasitidae.

Table 1 Guide to principal habitat preferences in the British and Irish species of Parasitinae. M = most frequent habitat, L = less frequent habitat, I = single isolated record, O = the only habitat recorded in the British Isles. Non-British habitats are marked 'x' where different or more frequent.

Habitat or association Parasitine species	Bumblebees	Other Hymenoptera	Scarabaeid or ground beetles	Other insects	Mammals or their nests	Birds or their nests	Seashore	Arable or grassland	Leaf-litter, mosses	Houseplant/greenhouse soil	Hay, straw, grain	Compost (rotting vegetation)	Manure, dung, sewage	Corpses/sexton-beetles	Fungi (including mushroom beds)
Parasitus coleoptratorum			M	I	L	L	L	L	M		I	M	M	I	I
Parasitus beta	x		L		Ix		I	M	x			Ix	x		
Parasitus consanguineus	I			L		L	L	x	L		M	M	M		L
Parasitus copridis			O												
Parasitus evertsi					I		L		I	L			L		I
Parasitus fimetorum	L		L		L	L	I		L			M	M	I	
Parasitus hyalinus						I		L				x	I		L
Parasitus insignis								O		x					
Parasitus kempersi							O								
Parasitus loricatus	I	L			M	M			L			M	L		M
Parasitus mustelarum			M		Lx						x	x	x		x
Vulgarogamasus burchanensis											Lx	I			
Vulgarogamasus immanis							O								
Vulgarogamasus kraepelini		I			M			L	M						L
Vulgarogamasus oudemansi					M	M			I						
Vulgarogamasus remberti					M	L									
Vulgarogamasus trouessarti							O								
Eugamasus magnus					I				M						
Eugamasus berlesei					M				M		I	L			
Eugamasus cavernicola					L				I						
Eugamasus crassitarsis								M	L						
Porrhostaspis lunulata					L		I	M	M			M			
Cornigamasus lunaris							L				M	M	M		
Parasitellus fucorum	M	L		L											
Parasitellus crinitus	M				I										
Parasitellus ignotus	M					I									
Parasitellus talparum	M				L										
Gamasodes spiniger				L	L	I	I	L	L		L			I	
Gamasodes bispinosus				I			Lx	x		I		x			
Gamasodes fimbriatus							O								
Poecilochirus carabi			L	L	L	L								M	
Poecilochirus austroasiaticus									x					M*	
Poecilochirus davydovae														O	
Poecilochirus subterraneus			L	L					I					M	
Trachygamasus ambulacralis					I		I	x	L				L		
Trachygamasus gracilis								O		x			x		

*See text, p. 358.


A
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Gnathosoma
Idiosoma
Opisthogaster
I
II
III
IV
pedipalp
chelicera
corniculus
tritosternum
presternal shield
endopodal shield
sternal shield
exopodal shield
peritreme
metasternal shield
stigma
genital shield
opisthogastric shield
anus
B
tarsus
apotele
tibia
al1
al2
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trochanter
sal. sty.
int. mal.
corn.
ant. hyp. s.
hyp.
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post. s.
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pcx. s.
hyp. dent.
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C
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III
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j5
s4
z5
d. hex.
j6
p. s.
s6
J2
S2
S3
J3
S4
S5
J4
J5
E
j1
j2
j3
z2
j4
r2
z4
r3
j5
s4
z5
d. hex.
r5
s5
s6
j6
R1
J1
Z1
S2
J2
m. s.
Z2
S3
J3
S4
Z3
J4
py. s.
S5
Z4
J5
F
z1
j1
j2
s1
p. s.
j3
s2
z2
r2
z3
j4
r3
s3
z4
r4
j5
s4
d. hex.
r5
z5
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s5
j6
z6
S1
Z1
J1
S2
J2
S3
Z2
J3
S4
J4
Z3
Z4
J5
o. s.

In all post-embryonic developmental stages the body is divided into two well-defined regions, the *gnathosoma,* or *capitulum,* which carries the *pedipalps* and *chelicerae,* and the *idiosoma* which bears the ambulatory appendages, the *legs* (Fig. 2A). The gnathosoma is articulated antero-ventrally to a cavity of the idiosoma, the *camerostome.*

Gnathosoma

The major part of the gnathosoma is formed by the enlarged *coxae* of the pedipalps which are extended dorsally and ventrally to form a sclerotized tube, the *basis gnathosomatica* (*bas. gnath.*) (Fig. 2B). The roof of the basis gnathosomatica is developed anteriorly to form the *gnathotectum,* or *tectum,* which in many species terminates in a strongly trispinate process (Figs 14D, 38J), or in some as a broad irregular triangle (Figs 22C, D, 24K). Ventrally the gnathosoma bears a median *hypognathal groove* (*hyp. gr.*) which is provided with transverse rows of *denticles* (*hyp. dent.*), and from two to four pairs of setae. In the larva only the *anterior hypostomatic* (*ant. hyp. s.*) and the *external posterior hypostomatic setae* (*ext. post. s.*) are present (Fig. 12F), but at the protonymph stage the *internal posterior hypostomatic* (*int. post. s.*) and the *palpcoxal setae* (*pcx. s.*) are added (Figs 12M, 13F, L, 14G).

The antero-ventral region of the gnathosoma, the *hypostome* (*hyp.*), bears, in addition to the hypostomatic setae, two pairs of anteriorly directed processes, the fringed *internal malae* (*int. mal.*) and the horn-like *external malae* or *corniculi* (*corn.*), the latter being probably of setal origin. In the genus *Cornigamasus,* the very long corniculi are grooved to accommodate the '*salivary*' *styli* (*sal. sty.*) which are ventro-lateral to the chelicerae (Fig. 41M), whereas in the remaining genera the corniculi are without grooves and the styli arise laterally or dorso-lateral to the chelicerae.

Chelicerae

The paired retractile chelicerae, which are located within the tubular region of the gnathosoma, are essentially feeding organs and are chelate (Fig. 2C). Each is divided into three segments or articles, the *basal article* (I) to which the retractor muscles are attached, the *middle article* (II) which terminates in the *fixed digit* (*f. d.*), and the *movable digit* (*m. d.*) (III) which is articulated ventrally with and opposes the fixed. Both digits are dentate, and in the male (Fig. 8L), the movable digit bears a sclerotized appendage, the *spermatodactyl* (*sp.*), which during copulation plays an important part in sperm transfer. In the Parasitidae the spermatodactyl is fused with the movable digit distally and a foramen, the *spermatotreme* (*sptr.*), is formed. Additionally each chelicera bears in the region of the fixed digit, two setae, the *dorsal seta* (*d. s.*) and the *pilus dentilis* (*p. d.*) (possibly a chemoreceptor), and two *lyriform fissures* (mechano-receptors), the *dorsal lyrifissure* (*d. lf.*) and the *lateral lyrifissure* (*l. lf.*). The *articulating* (or *arthrodial*) *membrane* (*arth.*) at the base of the movable digit is setiform.

Pedipalps

The pedipalps (or palps) have five free articulated *podomeres* or segments, *trochanter, femur, genu, tibia* and *tarsus* (Fig. 2B), and their chaetotaxy, which is constant in each developmental stage, may be shown by the following formula: larva – trochanter 0 (no setae), femur 4, genu 5, tibia 12, tarsus 11; protonymph – 1, 4, 5, 12, 15; deutonymph and adults – 2, 5, 6, 14, 15. Figures 12G, 12N and 13K show the chaetotaxy of a typical trochanter, femur and genu for larva, protonymph and adult respectively. Additionally the tarsus bears on its inner basal angle a movable flattened fork-like structure, an *ambulacrum*

Fig. 2 A diagrammatic representation of the venter of a female parasitine mite; B venter of the gnathosoma (excluding chelicerae); C lateral view of chelicera of a typical parasitine deutonymph or female; D–F basic nomenclature of dorsal sclerotization and chaetotaxy of a typical parasitine larva (D), protonymph (E) and deutonymph (F); I–IV, legs I–IV. Abbreviations in text, pp. 243–6.

or *apotele*. The *anterolateral setae* on the femur, *al*, and on the genu, al_1 and al_2, are variously modified and form useful key characters.

Idiosoma

Dorsal chaetotaxy and sclerotization

In general the Parasitinae differ conspicuously from the Pergamasinae in the diversity of the dorsal setae and in the degree of development of the dorsal sclerotization. In the Pergamasinae the dorsal setae are usually of uniform length and thickness, whereas in the majority of species of Parasitinae the setae are heterogeneous. Females of the Pergamasinae have an entire (*holodorsal*) shield which completely covers the idiosoma, whereas females of the Parasitinae generally have separate anterior (*podonotal*) and posterior (*opisthonotal*) shields, *p.s.* and *o.s.* respectively (Fig. 4A), or occasionally a *schizodorsal* shield in which the podonotal and opisthonotal shields are fused medially only and bear lateral incisions (Fig. 52L). The males of some species of Pergamasinae have a transverse suture between the podonotal and opisthonotal regions, whilst in others there is complete fusion. In the Parasitinae all males have a median transverse suture.

The dorsal chaetotactic pattern is widely used as a taxonomic criterion in the Mesostigmata, and the system followed in the present work is that of Lindquist and Evans (1965).

The basic nomenclature of the dorsal idiosomal chaetotaxy of a typical parasitine larva, protonymph and deutonymph are shown in figures 2D, E and F respectively. Four paired longitudinal rows of setae are designated as follows: dorsocentral (*j*, podonotal and *J*, opisthonotal), mediolateral (*z* and *Z*), lateral (*s* and *S*) and marginal (*r* and *R*). Setae *r1* and *Z5* do not occur in the Parasitidae. The deutonymphal chaetotaxy is retained in the adults. Setae *j5, z5* and *j6* form the *dorsal hexagon* (*d. hex.*) which may assist in establishing the boundary between the podonotal and opisthonotal regions in those Mesostigmata possessing a holodorsal shield, and is also a useful term to apply when describing the podonotal chaetotaxy. Setae *j1, z1* and *r3* are often referred to as the *vertical, paravertical* and *humeral* setae respectively. In those species in which the opisthonotal shield is hypertrichous, for example members of the genus *Parasitellus,* it is not always possible to define the *J, Z, S* and *R*-series (Fig. 44A).

The larva and protonymph are usually weakly sclerotized and the dorsal plates, although following a definite developmental sequence (Bhattacharyya, 1963, Evans and Till, 1979), may be poorly defined or apparently absent. In the larva (Fig. 2D) the podonotal region bears 10 pairs of setae of which nine are on the *podonotal shield* (*p. s.*), and the opisthonotal region bears eight pairs on unsclerotized cuticle. The protonymph (Fig. 2E) bears 11 pairs of setae on the podonotal shield and four pairs on the adjacent membrane, whilst the opisthonotal region bears 13 or 14 pairs, depending on whether *R1* is present or absent, and may or may not show partial sclerotization in the form of paired *mesonotal scutella* (*m. s.*) and a single *pygidial shield* (*py. s.*). The deutonymph (Fig. 2F) is much more heavily sclerotized than the preceding stages and the podonotal and opisthonotal shields are well defined. In most species the opisthonotal shield is almost as broad as the podonotal, but in some, for instance *Vulgarogamasus trouessarti* (Fig. 32A), it is noticeably narrower. Typically the podonotal region of the deutonymph bears 20 or more pairs of setae, almost all of which are on the shield, and the opisthonotal region bears 30 or so pairs with about half on the shield. As mentioned above species of *Parasitellus* bear additional setae on the opisthonotal shield. In the deutonymph of one species, *Vulgarogamasus immanis* (Fig. 24A), the podonotal shield is reduced and bears only 15–17 pairs of setae whilst the opisthonotal shield may bear as few as 11 pairs.

Venter

The ventral surface of the idiosoma is furnished with a number of shields whose progressive development, degree of sclerotization and the setae they bear, follow a regular sequence as described in the following paragraphs. The *endopodal* and *exopodal shields* (*end. sh.* and *ex. sh.*), which lie adjacent to the coxae of legs II-IV, are usually weakly developed or absent in the immature stages, although in the deutonymphs of *Poecilochirus* the endopodals are conspicuous at coxae IV (Fig. 55I). In the adults the exopodal shields are generally fused with the sclerotized peritrematal shields and the endopodals with the sternal/sternogenital shields, and may show as little more than strong borders to those regions (Fig 2A). Lying between the coxae of the first pair of legs, and immediately behind the gnathosoma, is the *tritosternum* (Fig. 2A), a sensory organ which is normally present in all post-embryonic stages of the Parasitidae, but may be reduced or absent in the males of some species of the Parasitinae.

Larva (Fig. 12B). This instar bears three pairs of legs. The sternal, or intercoxal, region bears three pairs of setae, *sternal setae* (*st.*) I–III, but there is no clear indication of a sternal shield. The *anal shield* (*a. s.*) is usually very weakly sclerotized and bears a pair of long *paranal* or *adanal setae* (*pa.*) and a single long *postanal seta* (*po.*). Each *anal valve* (*a. v.*) is provided with a short *euanal seta* (*eu.*). The remainder of the region posterior to the coxae of the third pair of legs, the *opisthogaster,* bears four pairs of setae. *Stigmata* and *peritremes* are absent.

Protonymph (Fig. 12J). At this stage the fourth pair of legs appears and the intercoxal region bears four pairs of setae, *st.* I–III on the scarcely discernible sternal shield, and *st.* V (homologous to the female genital setae) between the coxae of the fourth pair of legs. Also appearing now are two pairs of *sternal pores* (*pst.*), I and II. The anal shield is still weakly sclerotized, but the paired paranal setae and the postanal seta are considerably shorter than in the larva. There are no euanal setae. The remainder of the opisthogastric region bears six pairs of setae. A pair of stigmata and short peritremes are present.

Deutonymph (Fig. 13B). At this stage the *sternal shield* (*st. sh.*) is well developed and in most species is strongly sclerotized. The base of the tritosternum is normally flanked by a pair of triangular *presternal shields* (*pst. sh.*). Five pairs of sternal setae are present, *st.* IV (the *metasternal setae* of the female) having emerged at this stage in association with a third pair of pores, *pst.* III. The anal shield is strongly sclerotized and in most species bears only the paranal and postanal setae, although in some one or more pairs of opisthogastric setae may be located on the anterior margin of the shield (Figs 30B, 32B, C). The opisthogastric membrane may bear about ten to over 60 pairs of setae. Stigmata are present and the peritremes extend anteriorly to the region of the coxae of leg I. Small *metapodal shields* (*mp. sh.*) are present at this stage.

Male (Fig. 13H). The entire idiosoma is sclerotized except for ventrally the regions of attachment of the legs and gnathosoma (see also Fig. 11B). The *genital orifice* (*g. o.*) is situated at the anterior margin of the *sternogenital shield* (*stgen. sh.*) and the *genital lamina* (*g. l.*) may cover the base of the tritosternum, which may be reduced, or in some species, absent. The presternal shields can be absent or barely discernible. The ventral chaetotaxy resembles that of the female of the same species.

Female (Fig. 2A). The tritosternum is as in the deutonymph. The deutonymphal sternal shield bearing four pairs of setae and three pairs of pores has become a sternal shield bearing *st.* I–III and *pst.* I–II, and a pair of *metasternal shields* bearing *st.* IV and *pst.* III. The large triangular flap-like genital shield, which bears *st.* V, overlies the genital orifice and is hinged to the opisthogastric shield level with the posterior margin of coxae IV. Within the genital orifice are usually visible characteristically shaped endogynial processes (for example Fig. 14C). The extent of sclerotization of the opisthogastric shield varies between species and consequently the proportions of opisthogastric setae on the shield and on the surrounding membrane varies. The anal shield is fused with the opisthogastric shield.

Legs

Three pairs of legs are present in the larva and four pairs in the protonymph, deutonymph and adults. All legs have six segments or podomeres, namely – from the idiosoma – *coxa* (*cx.*), *trochanter* (*tr.*), *femur* (*fe.*), *genu* (*ge.*), *tibia* (*ti.*) and *tarsus* (*ta.*) (Fig. 2A), and all bear distally on the tarsus an *ambulacrum* (*am.*) comprising a *pretarsus* (*pt.*), a pair of *claws* (*cl.*) and a lobed *pulvillus* (*pulv.*) (Figs. 2A, 64I). The ambulacra of legs II–IV are stouter than on leg I. The first pair of legs are slender and are directed anteriorly and used primarily as a sensory appendage during locomotion. In the male leg II is modified for grasping the female during copulation and is usually considerably thickened, with the femur, genu and tibia bearing strong spurs ventrally (Fig. 13M). In some species the tarsus of leg II may also bear spurs or hypertrophied setae (Figs 34H, I).

Detailed studies on the numbers and distributional patterns of setae on the leg segments in the Mesostigmata have been conducted in recent years and these provide characters that are valuable at all levels of classification. Concise details of podomeric chaetotaxy are given by Evans and Till (1979), but in the present work the leg setae are mainly referred to in general terms, or individual setae are described when a particular species possesses conspicuously long, short or modified examples. Spurs or hypertrophied setae are generally figured.

So far as I am aware, in the deutonymph of only one British species of the Parasitinae, namely *Parasitus loricatus* (p. 283), is it possible to determine the sex of the future adult by distinct external morphological features, although frequently the developing adult is visible within the deutonymph when the specimen has been cleared for examination. I have no evidence to support the statement accredited to D. E. Johnston (Lundqvist and Micherdzinski, 1975) that the female deutonymphs of the Parasitidae have a star-shaped reticulated configuration posteriorly on the sternal shield, whilst the males have no such formation. Certainly this feature does not hold good for *P. loricatus.*

Family **PARASITIDAE** Oudemans

GAMASIDAE ['Gamasides'] Leach, 1815. *Trans. Linn. Soc. Lond.* **11:** 396.
PARASITINAE Oudemans, 1901. *Tijdschr. ned. dierk. Vereen.* **7:** 59.
POECILOCHIRIDAE Willmann, 1940. *Zool. Anz.* **130:** 215.
SAPROGAMASIDAE Willmann, 1949. *Veröff. Mus. nat.-Völker-Handelsk. Bremen* **A1:** 136.
EUGAMASINAE Hirschmann, 1962. *Acarologie* **5**(5): 39.

Summary of classification

The first major review of the family Parasitidae was Berlese's 'Monografia del genere *Gamasus* Latr.' published in 1906, in which he recognized the following eight subgenera: *Amblygamasus* Berlese, 1904*a*, *Eugamasus* Berlese, 1892*a*, *Gamasus* Latreille, 1802, *Halolaelaps* Berlese and Trouessart, 1889 (now in the family Halolaelapidae Karg, 1965), *Laelogamasus* Berlese, 1905 (now in the family Rhodacaridae Oudemans, 1902*b*), *Ologamasus* Berlese, 1906 (*nec* Berlese, 1888), *Pergamasus* Berlese, 1904*a*, and *Trachygamasus* Berlese, 1904*a*. Most subsequent workers, for example Baker and Wharton (1952), who covered the world fauna, and Evans (1957), who dealt with the British fauna, have based their classifications on Berlese's monograph.

More recently, Micherdzinski (1969), in his extensive review of the family, recognized the genera *Gamasodes* Oudemans, 1939*a*, *Holoparasitus* Oudemans, 1936 (= *Ologamasus*), *Oocarpais* Berlese, 1916, *Parasitus* Latreille, 1795 (including *Eugamasus*), *Pergamasus*, *Poecilochirus* G. and R. Canestrini, 1882, and *Saprogamasus* Willmann, 1949*b* (= *Trachygamasus*). *Holoparasitus, Parasitus* and *Pergamasus* he divided into species groups.

Holzmann (1969)* restricted *Parasitus* to *Acarus fucorum* De Geer, 1778, plus a new species, *Parasitus willmanni.* The other genera she recognized are *Eugamasus, Gamasodes, Ologamasus, Pergamasus, Poecilochirus,* and *Trachygamasus.* The monotypic Indian genus *Oocarpais* she considered to be a synonym of *Pergamasus.* The description of the new genus *Willmanniella* Götz, 1969, with its type species *W. fallax* sp. nov., is taken from a thesis of 1952 at the Zoologischen Institut, Erlangen, and is incorporated into Holzmann's text where it is considered to be a synonym of *Trachygamasus.*

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*This paper is a summary of the author's 1955 thesis from the Zoologischen Institut, Erlangen, which is deposited in the Bayerischen Staatsbibliotek, Munich.

Tichomirov (1969) considers previous views on the separation of *Parasitus* and *Eugamasus* and proposes the division of *Parasitus* into five subgenera, *Coleogamasus* Tich., *Eugamasus, Neogamasus* Tich., *Parasitus* and *Vulgarogamasus* Tich. *Neogamasus* is not further considered here as so far none of the species assigned to it has been recorded in the British Isles.

Karg (1971) favours the subfamily Parasitinae of the Eugamasidae Hirschmann, 1962 and, like Micherdzinski (1969), combines *Parasitus* with *Eugamasus*, but does not group the species. He recognizes *Gamasodes, Holoparasitus, Parasitus, Pergamasus, Poecilochirus* and *Trachygamasus.*

Juvara-Bals (1972) proposed the division of the Parasitidae into two subfamilies, the Parasitinae and the Pergamasinae, and Evans and Till (1979), in adopting this separation, have produced a practical classification for the British Parasitinae in which they recognize the following nine genera: *Cornigamasus* Evans and Till, *Eugamasus, Gamasodes, Parasitellus* Willmann, 1939*b*, *Parasitus, Poecilochirus, Porrhostaspis* Müller, 1859, *Trachygamasus* and *Vulgarogamasus.* In the Pergamasinae they include the following five genera: *Amblygamasus, Holoparasitus, Paragamasus* Hull, 1918, *Pergamasellus* Evans, 1957, and *Pergamasus.* Most of the British Pergamasinae were revised by Bhattacharyya (1963) in his review of *Pergamasus* s. lat., although additional species have since been collected. The remaining British genus of this subfamily, namely *Holoparasitus*, is at present in course of revision (Hyatt, in prep.). However, Athias-Henriot has, since 1967, produced a series of papers on the Parasitidae in which a number of new genera and subgenera are proposed and others are redefined. Where her changes involve British species, these are cited in the relevant synonymy, but for practical purposes I am following the generic concepts of Evans and Till (1979).

The two subfamilies may be separated as follows:

1 Females with separate podonotal and opisthonotal shields, or occasionally a schizodorsal shield (Fig. 52L); tritosternum of male normal, similar to that of the female (Fig. 39I), or modified (Fig. 6B), or absent; setae *z5* of dorsal hexagon in adults and deutonymph may differ markedly in form from *j5* and *j6* (Fig. 3A), or only slightly (Fig. 26A), or the three pairs of setae may be homogeneous (Fig. 32A) . . subfamily **PARASITINAE** Oudemans, 1901

– Females with dorsal shield entire; tritosternum of male always biramous with a reduced base which is covered by the genital lamina; all setae of dorsal hexagon, that is *z5, j5* and *j6*, of similar length and form . . . subfamily **PERGAMASINAE** Juvara-Bals*, 1972

Key to the British genera of Parasitinae based on the deutonymphs and adults

1 Setae al_1 and al_2 of palp genu in deutonymph and adults bifid (Fig. 35K) ***EUGAMASUS*** Berlese, 1892*a* (p.310)

– Setae al_1 and al_2 of palp genu entire, spatulate (Fig. 58E) or setiform (Fig. 15E) . . 2

2 Opisthogaster hypertrichous, typically with more than 40 pairs of setae (Figs 48B, H, 49B). Associated with *Bombus* . . . . ***PARASITELLUS*** Willmann, 1939*b* (p. 327)

– Opisthogaster with rarely more than 30 pairs of setae 3

3 Corniculi in deutonymph and adults long, slender, parallel and extending beyond anterior margin of palp trochanter; corniculi grooved to accommodate 'salivary' styli which arise ventro-lateral to the chelicerae (Fig. 41M); anterior margin of opisthonotal shield distinctly concave in deutonymph and female (Fig. 41A, H) ***CORNIGAMASUS*** Evans and Till, 1979 (p. 324)

– Corniculi short, not extending to anterior margin of palp femur, lacking grooves; 'salivary' styli arising lateral or dorso-lateral to chelicerae; anterior margin of opisthonotal shield not concave 4

4 Genital shield of female elongate, tricuspid anteriorly (Fig. 40B); male chelicerae asymmetrical due to presence of digitiform process on the spermatodactyl of the right chelicera (Fig. 39L, M) . . . ***PORRHOSTASPIS*** Müller, 1859 (p. 320)

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*Evans and Till, 1979 give Athias-Henriot, 1973.

– Genital shield of female subtriangular in outline, never tricuspid anteriorly; male chelicerae symmetrical 5

5 Seta *al* of palp femur spatulate (Fig. 57E) or setiform (Fig. 51E), at the most spiculate distally (Fig. 64G); idiosoma less than 2000 μm 6

– Seta *al* of palp femur bifid (Fig. 5E) or with one or more distinct slender processes (Fig. 26F); if spatulate however (*Vulgarogamasus immanis*, Fig. 25F) idiosoma greater than 2000 μm in length 8

6 Setae *z5* of dorsal hexagon of female similar in type to *j6*; with distinct podonotal and opisthonotal shields in female (these may be partly fused, Fig. 59A); corniculi of male usually hooked (Fig. 56F); tritosternum normal; sternal shield of deutonymph with dark transverse band (Fig. 57B) . . ***POECILOCHIRUS*** G. & R. Canestrini, 1882 (p. 349)

– Setae *z5* of dorsal hexagon of female differing in length and form from *j6* (Fig. 9A); if similar, then female with schizodorsal shield (Fig. 52L); male corniculi not hooked; tritosternum of male absent or modified, never biramous 7

7 Female with two dorsal shields or with schizodorsal shield; suture between metasternal and sternal shields conspicuous and forming an inverted V (Fig. 51B); ambulacra of legs II–IV with lateral lobes of pulvillus inconspicuous, rounded; leg II of deutonymph with spurs (Fig. 52G) . . . . ***GAMASODES*** Oudemans, 1939*a* (p. 340)

– Female with two dorsal shields; metasternal shields fused with sternal shield or separated by a complete or incomplete transverse suture (Fig. 64D); ambulacra of legs II–IV with lateral lobes of pulvillus long acuminate (Fig. 64I); leg II of deutonymph without spurs ***TRACHYGAMASUS*** Berlese, 1904*a* (p. 363)

8 With few exceptions, setae *z5* of dorsal hexagon markedly different in form from *j5* and *j6*, usually stout and setose; tritosternum of male absent or variously modified (Fig. 21G), if biramous, base closely associated with genital orifice (Fig. 8J) ***PARASITUS*** Latreille, 1795 (p. 256)

– Setae of dorsal hexagon essentially similar in form, none outstandingly different (Fig. 24H); tritosternum normal in both sexes, base never closely associated with the genital orifice of the male (Fig. 26I) . . . . ***VULGAROGAMASUS*** Tichomirov, 1969 (p. 290)

Synonymy

The synonymy given is not intended to be exhaustive or complete. The principal synonyms only are given together with those that are relevant to literature on the British and Irish fauna. The interpretations of European species as given by Holzmann (1969), Micherdzinski (1969) and Karg (1971) are generally accepted. However, it must be emphasized that the key characters chosen by these authors are in some cases variable. This has been proved by examination of series of specimens which show variations that would place them in different parts of their keys, and thus conspecific specimens would be identified as belonging to different species.

Key to deutonymphs

1 Leg II with conspicuous ventral spurs, usually on the femur, genu tibia and tarsus (Fig. 50G); presternal shields conspicuous, elongate, and sternal shield of characteristic outline (Fig. 50B); dorsal setae mainly short, some may be stouter and pilose distally ***Gamasodes*** 2

– Leg II without spurs; presternal and sternal shields variously formed (Figs 21B, 48B); dorsal setae of extreme lengths (Figs 3A, 39A, 46A) 4

2 Femur II with two ventral spurs, tibia with none (Fig. 52G); dorsal setae *j1* and *r3* stout and pilose distally, remaining setae simple ***Gamasodes bispinosus*** (Halbert) (p. 345)

– Femur and tibia II with one ventral spur each (Fig. 50G); more than two pairs of dorsal setae stout and pilose 3

3 Ventral spur on femur II straight (Fig. 53D); all simple dorsal setae very short, rarely exceeding 20 μm (Fig. 53A); lateral prongs of tectum poorly developed ***Gamasodes fimbriatus*** Karg (p. 347)

– Ventral spur on femur II thumb-shaped (Fig. 50G); dorsal setae longer (Fig. 50A); lateral prongs of tectum well developed (Fig. 50C) ***Gamasodes spiniger*** (Trägårdh) (p. 341)

4 Sternal shield with a transverse granular band between setae I and II (Fig. 55I); fixed digit of chelicera with a distal membraneous process which may be rudimentary (Figs 55K, 60D) ***Poecilochirus*** 5

– Sternal shield without granular area; fixed digit of chelicera without membraneous process 8

5 Transverse granular area of sternal shield extends posteriorly to form a narrow border (Fig. 62B) 6

– Transverse granular area of sternal shield not extending to setae III (Fig. 55I) 7

6 Majority of the dorsal setae long and reaching or passing the bases of the next seta (Fig. 62A) ***Poecilochirus subterraneus*** (Müller) (p. 361)

– Majority of dorsal setae short or very short, few only reaching the base of the next seta (Fig. 60A) ***Poecilochirus davydovae*** sp. n. (p. 358)

7 Podonotal shield not exceeding 450 μm, opisthonotal shield *c.* 300 μm; setae *j5* and *J1* extending well beyond the bases of the next setae (Fig 57A); fixed digit of chelicera with distal membraneous process rudimentary (Fig. 57D) ***Poecilochirus austroasiaticus*** Vitzthum (p. 355)

– Podontal shield exceeding 550 μm, opisthonotal shield exceeding 400 μm; setae *j5* and *J1* reaching but rarely passing the bases of the next setae (Fig. 55H); fixed digit of chelicera with membraneous process well developed ***Poecilochirus carabi*** G. & R. Canestrini (p. 350)

8 Dorsal shields characteristically outlined; posterior margin of podonotal shield strongly convex medially and anterior margin of opisthonotal shield strongly concave medially; all dorsal setae relatively short (Fig. 41A); corniculi long and slender (Fig. 41M), reaching at least the mid-point of the palp femur; tectum a single central prong with denticulate sloping margins (Fig. 41C) ***Cornigamasus lunaris*** (Berlese) (p. 324)

– Dorsal shields otherwise; corniculi normally much shorter, triangular (Fig. 10F) and only reaching the mid-point of the palp trochanter 9

9 Dorsal setae overall without extreme differences in length or stoutness although *j1, z5* and *r3* are generally the longest 13

– Some dorsal setae in addition to *j1, z5* and *r3* conspicuously stouter and longer than the remaining setae which are generally very short (Figs 10A, 21A) 10

10 Podonotal shield with setae *s6* unusually long; opisthonotal shield with 14 pairs of setae, *Z3* 250 μm or longer (Fig. 10A); tectum with short broad central process and small hornlike lateral prongs (Fig. 10C) ***Parasitus copridis*** Costa (p. 267)

– Seta *s6* short; opisthonotal shield with more than 14 pairs of setae, *Z3* not exceeding 150 μm (Fig. 3A) 11

11 Tectum quinque-spinate (Fig. 3C); seta *j4* long and pilose distally (Fig. 3A); opisthonotal shield with 16 pairs of setae; sternal shield blunt posteriorly and with setae *st.* IV situated near the posterior margin (Fig. 3B) ***Parasitus coleoptratorum*** (Linnaeus) (p. 256)

– Tectum trispinate; seta *j4* not conspicuously long; opisthonotal shield with 15 or 17 pairs of setae; sternal shield tapered posteriorly 12

12 Tectum with median spine three times as long as lateral spines (Fig. 21C); opisthonotal shield with 17 pairs of setae of which one pair, *Z3*, are stout and pilose (Fig. 21A); sternal shield broad, characteristically ornamented narrowing abruptly behind *pst.* II (Fig. 21B) ***Parasitus mustelarum*** Oudemans (p. 288)

– Tectum with median spine less than twice as long as lateral spines (Fig. 17C); opisthonotal shield with 15 pairs of setae of which *Z3* are long and stout and *J5* are thornlike and with a small conspicuous median mark slightly anterior to *J5* (Fig. 17A); sternal shield narrower, of more usual proportions (Fig. 17B); restricted to the seashore ***Parasitus kempersi*** Oudemans (p. 280)

13 Opisthogastric membrane densely setose, with over 40 pairs of setae (Fig. 48B); normally associated with *Bombus* spp. and their nests 14

– Opisthogastric membrane with less than 30 pairs of setae 17

14 Sternal shield broad and with conspicuous longitudinal striations within the laterally arranged reticulations (Fig. 42B); opisthonotal shield triangular, clearly narrower than the podonotal and with 15 pairs of setae (Fig. 42A) ***Parasitellus fucorum*** (De Geer) (p. 328)

– Sternal shield narrower, without striations; opisthonotal shield with more than 20 pairs of setae 15

15 Opisthogastric setae very short, generally not exceeding 35 µm (Fig. 48B); opisthonotal shield usually with 24 to 30 pairs of setae, *J*-series without additional setae (Fig. 48A) ***Parasitellus talparum*** (Oudemans) (p. 337)

– Opisthogastric setae clearly longer; opisthonotal shield usually with more than 35 pairs of setae some of which are situated among the *J*-series (Fig. 44A) 16

16 Podonotal shield with an additional seta lying between *r5* and *s6*; additional setae among the *J*-series shorter than *J1*–*J3* (Fig. 46A); lateral margins of tectum toothed (Fig. 46C); anal shield with the normal three setae (Fig. 46B) ***Parasitellus ignotus*** (Vitzthum) (p. 334)

– Podonotal shield without additional setae between *r5* and *s6*; additional setae among the *J*-series as long as the *J*-setae; lateral margins of tectum smooth (Fig. 44A); anal shield with additional setae (Fig. 44B) . . ***Parasitellus crinitus*** (Oudemans) (p. 331)

17 Anal shield with more than the usual three setae 18

– Anal shield with only three setae 22

18 Opisthonotal shield with 22 pairs of setae ***Eugamasus berlesei*** Willmann (p. 313)

– Opisthonotal shield with 15 or less pairs of setae 19

19 Opisthonotal shield conspicuously small within the opisthonotal region and of characteristic shape (Figs 24A, 32A); tectum broad and strongly denticulate (Figs 24D, 32D); large species, considerably more than 1 mm; restricted to the seashore 20

– Opisthonotal shield of more normal proportions; tectum simple, trispinate (Fig. 16C); size less than 1 mm 21

20 Podonotal shield over 800 µm; opisthonotal shield usually over 500 µm; median part of tectum tapered (Fig. 24A); anal shield with one pair of preanal setae (Fig. 24B) ***Vulgarogamasus immanis*** (Berlese) (p. 292)

– Podonotal shield less than 600 µm; opisthonotal shield less than 400 µm; median part of tectum broad, denticulate and similar to lateral elements (Fig. 32D); anal shield with at least four preanal setae (Fig. 32B) ***Vulgarogamasus trouessarti*** (Berlese) (p. 307)

21 The majority of the dorsal setae, on both shields and membrane, long and slender, reaching beyond the bases of the succeeding setae, opisthonotal shield with 14 pairs of setae (Fig. 30A); posterior opisthogastric and extra-anal setae also reaching beyond the bases of the succeeding setae; postanal seta twice the length of the more slender paranal setae (Fig. 30B) ***Vulgarogamasus remberti*** (Oudemans) (p. 304)

– Dorsal setae, with few exceptions, short, not reaching the bases of the succeeding setae; opisthonotal shield with 13 pairs of setae (Fig. 16A); opisthogastric and anal setae much shorter (Fig. 16B) . . . . . . ***Parasitus insignis*** (Holzmann) (p. 279)

22 Lateral prongs of trispinate tectum broad and strongly bifurcate (Fig. 8D); presternal shields conspicuous, elongate, wider than the anterior margin of the sternal shield; sternal shield usually fragmented anteriorly, with *st.* I situated on isolated areas (Fig. 8B); colour normally dull brown . . ***Parasitus consanguineus*** Oudemans & Voigts (p. 263)

– Lateral prongs of trispinate tectum not strongly bifurcate; presternal shields small or rudimentary and sternal shield normal, entire, with *st.* I not isolated (Fig. 26B) . . 23

23 Dorsal setae, excluding *z1*, *s1*, *s2*, *r2* and *r3*, markedly homogeneous, with *j4* and *z5* not conspicuously longer than the adjacent setae 24

– Dorsal setae not homogeneous (Figs 13A, 39A) 27

24 Dorsal setae short, majority on podonotal shield not reaching the base of the succeeding seta (Fig. 63A); ambulacra of legs II–IV with lateral lobes acute (Fig. 63E) ***Trachygamasus*** (p. 363)

– Dorsal setae long, majority on podonotal shield passing the base of the succeeding seta (Fig. 19A); ambulacra without acute lobes 25

25 Tectum with lateral prongs either broad and tapering (Fig. 19D) or if slender, with central part characteristically lobed (Fig. 19C); all dorsal setae, except *z1*, *s1*, *s2* and *r2*, finely pilose (Fig. 19A) . . . . ***Parasitus loricatus*** (Wankel) (p. 283)

– Tectum with central prongs pointed and lateral prongs slender (Fig. 28C); few dorsal setae clearly pilose 26

26 Podonotal shield over 470 µm long; opisthonotal shield over 310 µm long; sternal shield over 310 µm long . . . . . . ***Vulgarogamasus oudemansi*** (Berlese) (p. 300)

– Podonotal shield less than 450 µm long; opisthonotal shield less than 290 µm long; sternal shield less than 290 µm long ***Vulgarogamasus kraepelini*** (Berlese) (p. 297)

27 Anterolateral seta on palp femur deeply bifurcate (Fig. 5E); opisthonotal shield bearing 15 pairs of setae (Fig. 5A) 28

– Anterolateral seta on palp femur not deeply bifurcate (Fig. 39G); opisthonotal shield with 10 pairs of setae (Fig. 39A) . . . ***Porrhostaspis lunulata*** Müller (p. 320)

28 Setae *z5* and *j4* not longer than *z4, s4, s5* and *z6,* and *z5* not reaching the base of *z6* (Fig. 15A); sternal shield about 180 *μ*m long ***Parasitus hyalinus*** (Willmann) (p. 277)

– Setae *z5* and *j4* longer and stouter than adjacent setae and *z5* reaching the posterior margin of the podonotal shield (Fig. 13A); sternal shield more than 200 *μ*m long 29

29 Seta *s5* as stout as *z5* (Fig. 5A); sternal shield less than 250 *μ*m in length ***Parasitus beta*** Oudemans & Voigts (p. 260)

– Seta *s5* much finer than *z5* (Fig. 13A); sternal shield over 260 *μ*m in length ***Parasitus fimetorum*** (Berlese) (p. 271)

Key to males

1 Opisthonotal region of dorsum with more than 70 pairs of setae (Fig. 48G); normally associated with *Bombus* spp. and their nests 2

– Opisthonotal region of dorsum with less than 70 pairs of setae (Figs 38A, 39H) . . 5

2 Podonotal setae generally long and reaching well beyond the bases of the succeeding setae (Fig. 48G) 3

– A few of the podonotal setae reaching beyond the bases of the succeeding setae (Fig. 44G) 4

3 Opisthonotal region with additional setae between *J1–J3* (Fig. 46G); opisthogastric region with *c.* 80 pairs of setae; postanal seta slightly longer than paranals (Fig. 46H) ***Parasitellus ignotus*** (Vitzthum) (p. 334)

– No additional setae between *J1–J3*; opisthogastric region with *c.* 50 pairs of setae; postanal seta clearly longer and stouter than paranals (Fig. 48H) ***Parasitellus talparum*** (Oudemans) (p. 337)

4 Opisthonotal region bearing up to 80 pairs of setae and with additional setae within the *J*-series (Fig. 44G); opisthogastric setae long, anal setae subequal (Fig. 44H). ***Parasitellus crinitus*** (Oudemans) (p. 331)

– Opisthonotal region with up to 100 pairs of setae; no additional setae in the *J*-series (Fig. 42H); opisthogastric setae shorter, postanal seta stout and up to three times as long as the paranals (Fig. 42I) . . . . ***Parasitellus fucorum*** (De Geer) (p. 328)

5 Podonotal setae *j1, j4, z5* and *r3,* and usually at least one pair of opisthonotal setae, frequently stout and pilose and clearly longer than the remaining setae except the short *z1, s1, s2, r2* series 6

– With the exception of *z1, s1, s2, r2* and *r3* all dorsal setae of approximately equal length 20

6 Tritosternum present, either well developed (Fig. 41E) or rudimentary (Figs 3G, 53F) . 7

– Tritosternum absent 18

7 Tritosternum well developed although the base may be short (Fig. 11B) 8

– Tritosternum rudimentary with the base and/or the laciniae atrophied (Figs 3G, 21G) . 11

8 Opisthonotal region with less than 25 pairs of setae (Fig. 11A); tectum broad and usually trispinate (Figs 11C, 39J) 9

– Opisthonotal region with more than 30 pairs of setae (Fig. 58A); tectum produced into a single tapered process (Figs 56C, 58C) 10

9 Podonotal region with setae *j1, j4, z5* and *r3* stout and finely pilose and much longer than the remaining setae; with a pair of large conspicuous circular pores posterolaterally (Fig. 11A); corniculi sessile, plain (Fig. 11E) . . ***Parasitus evertsi*** Oudemans (p. 269)

– Podonotal region with setae *j1, j4* and *z5* not excessively longer than the remaining setae; circular pores absent (Fig. 39H); corniculi stalked, slender and notched on the inner margins (Fig. 39O) . . . . . . ***Porrhostaspis lunulata*** Müller (p. 320)

10 Large species, idiosoma exceeding 1200 *μ*m; opisthonotal and opisthogastric setae relatively short, few reaching beyond the bases of the succeeding setae (Fig. 56A, B); setae on palp trochanter arising from strong tubercles (Fig. 56E) ***Poecilochirus carabi*** G. & R. Canestrini (p. 350)

– Smaller species, idiosoma not exceeding 850 *μ*m; opisthonotal and opisthogastric setae long, the majority reaching well beyond the bases of the succeeding setae (Fig. 58A, B); palp trochanter lacking strong tubercles (Fig. 58E) ***Poecilochirus austroasiaticus*** Vitzthum (p. 355)

11 Trochanter of pedipalp with two strong tooth-like protuberances ventrally (Fig. 3J); tectum with a strong tapered prominence arising from a broad square base (Fig. 3H) ***Parasitus coleoptratorum*** (Linnaeus) (p. 256)

– Trochanter of pedipalp normal; tectum otherwise 12

12 Tectum trispinate (Figs 6C, 13I) 13

– Tectum with prominent median process (Figs 21C, 10H) 17

13 Anterolateral seta on palp femur strongly bifid 14

– Anterolateral seta on palp femur serrated or notched (Figs 53I, 64G) 16

14 Corniculi deeply cleft (Fig. 13L); tectum with converging long slender tines (Fig. 13I) ***Parasitus fimetorum*** (Berlese) (p. 271)

– Corniculi entire; tines of tectum shorter, not converging (Fig. 8K) 15

15 Idiosoma *c.* 600 µm in length; *Z1* and *Z3* stout; *J1–J4* each reaching the bases of the succeeding setae (Fig. 6A); spurs on leg II slender, those on the femur greatly reduced and separated (Fig. 6G) . . . . ***Parasitus beta*** Oudemans & Voigts (p. 260)

– Idiosoma exceeding 800 μm in length; setae *s5*, *Z1* and *Z3* slender; *J1–J4* short not reaching the bases of the succeeding setae (Fig. 8I); spurs on leg II shorter, main spur on the femur strong and contiguous with auxiliary spur (Fig. 8O) ***Parasitus consanguineus*** Oudemans & Voigts (p. 263)

16 Leg II with spurs (Fig. 53K); opisthogastric region with two pairs of the posterior setae stout and pilose distally (Fig. 53F); tectum with median tine broad, lateral tines short, pointed (Fig. 53G); dorsum with setae *j1*, *j4*, *z5*, *r3*, *Z1* and *Z3* very stout and pilose distally, remainder very short (Fig. 53A) . . ***Gamasodes fimbriatus*** Karg (p. 347)

– Leg II without spurs; opisthogastric setae simple; tectum with median tine trifid and pectinate distally (Fig. 64E); dorsum with setae *j4*, *z5*, *r3*, *Z1* and *Z3* pilose distally and slightly stouter than the remaining setae (Figs 64A, 63F) ***Trachygamasus*** (p. 363)

17 Large species, idiosoma exceeding 1100 μm; tectum unusually shaped, comprising a single broad process with a pair of lateral branches (Fig. 10H); corniculi cleft (Fig. 10J) ***Parasitus copridis*** Costa (p. 267)

– Smaller species, idiosoma *c.* 900 μm; tectum with median tine flanked on each side basally by dentate cusps (Fig. 21H); corniculi not cleft (Fig. 21J) ***Parasitus mustelarum*** Oudemans (p. 288)

18 Corniculi long and slender (Fig. 41M), reaching the midpoint of the palp femur; tectum with strong central tine and dentate base (Fig. 41J); transverse suture between opisthonotal and podonotal regions undulating strongly as in the female (Fig. 41H) ***Cornigamasus lunaris*** (Berlese) (p. 324)

– Corniculi short, not reaching beyond palp trochanter; tectum otherwise; dorsal suture not strongly undulating 19

19 Idiosoma averaging 750 μm long; podonotal region with setae *j1*, *j4*, *z5* and *r3* stout and distally-pilose, measuring up to 50 μm, remaining setae all very short and fine, maximum length 23 μm; opisthonotal region with *c.* 40 pairs of setae of which 4–5 pairs are stout and pilose distally (Fig. 50H); anal setae short (Fig. 50I) ***Gamasodes spiniger*** (Trägårdh) (p. 341)

– Idiosoma averaging 1050–1100 µm long; podonotal region with setae *j1*, *j4*, *z5* and *r3* long, stout and finely pilose, and *z1*, *r2* and *s5* thornlike, the remainder fine; opisthonotal region with *c.* 30 pairs of setae of which *Z3* are long stout and finely pilose, and *J1*, *Z1*, *S2* and several posterior to *Z3* are thornlike, the remainder being fine (Fig. 17G); postanal seta stout, pilose and up to three times as long as the paranals; restricted to the seashore ***Parasitus kempersi*** Oudemans (p. 280)

20 Tectum a variable irregularly-toothed prominence (Figs 24K, 32J, K); restricted to the seashore 21

– Tectum otherwise 22

21 Large species, idiosoma exceeding 2000 μm; tritosternum with rather short base (Fig. 24I); opisthonotal region with approximately 45 pairs of setae ***Vulgarogamasus immanis*** (Berlese) (p. 292)

– Smaller species, idiosoma less than 1200 μm; tritosternum with normal long base (Fig. 32I); opisthonotal region with approximately 32 pairs of setae ***Vulgarogamasus trouessarti*** (Berlese) (p. 307)

22 Corniculi cleft (Fig. 19M); accessory spur on femur II deeply bifid, V-shaped (Fig. 19N) **Parasitus loricatus** (Wankel) (p. 283)
– Corniculi entire; accessory spur on femur II single or irregularly formed 23
23 Palp trochanter with proximal seta unusually stout, arising from a conspicuous protuberance (Fig. 28L, M); tectum a broad triangular plate with a single pair of lateral basal teeth (Fig. 28I) . . . **Vulgarogamasus oudemansi** (Berlese) (p. 300)
– Setae on palp trochanter normal; tectum otherwise 24
24 Tectum of characteristic outline (Fig. 26J) **Vulgarogamasus kraepelini** (Berlese) (p. 297)
– Tectum otherwise 25
25 Dorsal setae very short, few reaching the bases of the succeeding setae (Figs 52H, 61A) . 26
– Dorsal setae longer, many reaching the bases of the succeeding setae (Figs 31A, 38A) . 27
26 Podonotal setae *r3* and *z5* longer than the remaining setae (Fig. 61A), dorsum less than 700 µm . . . . **Poecilochirus davydovae** sp. n. (p. 358)
– Setae *r3* and *z5* not conspicuously longer than the remaining setae (Fig. 52H), dorsum more than 750 µm . . . . . . **Gamasodes bispinosus** (Halbert) (p. 345)
27 Tectum typically trispinate although the central prong may be rudimentary (Figs 34C, D, 31C) 28
– Tectum otherwise (Figs 16F, 22C, D) 31
28 Gnathosoma with a pair of small rounded protuberances lying inwards from the bases of the palpcoxal setae (Fig. 34G) 29
– Venter of gnathosoma without protuberances 30
29 Tarsus II with a strong apically-directed spine (Fig. 34H, I); fixed digit of chelicera with a tooth-like projection at its base (Fig. 34E); large species, idiosoma ranging from 1350–1660 µm . . . . **Eugamasus magnus** (Kramer) (p. 310)
– Tarsus II with strong setae only (Fig. 35M); fixed digit of chelicera more slender, without a tooth-like projection at its base (Fig. 35J); smaller species, idiosoma ranging from 1150–1350 µm . . . . . . **Eugamasus berlesei** Willmann (p. 313)
30 Large species, idiosoma exceeding 1500 µm; tectum with centre prong considerably longer than lateral prongs (Fig. 38J); anal setae short, subequal (Fig. 38B) **Eugamasus crassitarsis** (Halbert) (p. 318)
– Small species, idiosoma not exceeding 550 µm; tectum trispinate, but the centre prong may be rudimentary (Fig. 31C); postanal seta at least twice as long as the paranals (Fig. 31B) **Vulgarogamasus remberti** (Oudemans) (p. 304)
31 Femur II with main spur robust and directed apically, accessory spur blunt (Fig. 16I); tectum narrow and with three to five teeth on its anterior margin (Fig. 16F) **Parasitus insignis** (Holzmann) (p. 279)
– Femur II with main and accessory spurs projecting at right angles to the segment (Fig. 22H); tectum a broad triangular plate with a pair of lateral teeth (Fig. 22C, D) **Vulgarogamasus burchanensis** (Oudemans) (p. 290)

Key to females

1 Division between sternal and metasternal shields transverse, sometimes obscure (Fig. 64D); lateral lobes of pulvilli acuminate (Fig. 64I) . . . **Trachygamasus** (p. 363)
– Division between sternal and metasternal shields oblique (Figs 38I, 51B), occasionally indistinct (Fig. 15H); ambulacra without such acute lobes 2
2 Opisthogastric shield with 20 or more pairs of setae (Figs 45B, 47B); normally associated with *Bombus* spp. and their nests 3
– Opisthogastric shield with usually not more than 12 pairs of setae (Figs 38I, 41I) . . 6
3 Opisthogastric shield with less than 25 pairs of setae (Fig. 45B) **Parasitellus crinitus** (Oudemans) (p. 331)
– Opisthogastric shield with more than 30 pairs of setae (Fig. 43B) 4
4 Opisthogastric shield with about 16 long and finely pilose setae situated medially, the remainder, together with those on the surrounding membrane, short and simple (Fig. 49B) **Parasitellus talparum** (Oudemans) (p. 337)
– Opisthogastric setae homogeneous 5

5 Dorsal and ventral setae simple, generally long and passing the bases of the succeeding setae (Fig. 47A, B); tectum trispinate (Fig. 47C) ***Parasitellus ignotus*** (Vitzthum) (p. 334)

– Dorsal and ventral setae considerably shorter, stouter and pilose (Fig. 43A, B); tectum bispinate (Fig. 43C) . . . . ***Parasitellus fucorum*** (De Geer) (p. 228)

6 Podonotal setae *j1, j4, z5* and *r3* frequently stout and pilose and clearly longer than the remaining setae (Figs 11G, 14A) 7

– Podonotal setae relatively homogeneous (Figs 36A, 56H), or with at least half longer than the remainder (Figs 15G, 40A) 17

7 Tectum a long tapered prong arising from a denticulate base (Figs 4C, 41J) . . . 8

– Tectum trispinate, rarely bispinate 9

8 Opisthonotal shield with 12 pairs of setae; corniculi long and slender (Fig. 41M), reaching the midpoint of the palp femur, opisthogastric shield with 7 pairs of setae (Fig. 41I) ***Cornigamasus lunaris*** (Berlese) (p. 324)

– Opisthonotal shield with about 35 pairs of setae; corniculi normal (Fig. 4F), not reaching beyond palp trochanter; opisthogastric shield with 10–12 pairs of setae (Fig. 4B) ***Parasitus coleoptratorum*** (Linnaeus) (p. 256)

9 Genital shield conspicuously broad and shallow, abruptly tapering anteriorly; presternal shields granular, broad and well developed (Fig. 54C); short dorsal setae rarely exceeding 25 μm (Fig. 51A) 10

– Genital shield narrower and deeper; presternal shields less well developed, may be rudimentary or absent (Figs 11H, 18A); dorsal setae never as short 11

10 Found exclusively in seashore debris . ***Gamasodes fimbriatus*** Karg (p. 347)

– Found in vegetation, compost, nests of mammals and birds ***Gamasodes spiniger*** (Trägårdh) (p. 341)

11 Anterolateral seta on palp femur deeply bifurcate (Fig. 14F) 12

– Anterolateral seta on palp femur not bifurcate (Fig. 18E) 14

12 Posterior hypostomatic setae straight, externals almost twice the length of the internals (Fig. 9F); sternal setae I forked distally and arising from small platelets (Fig. 9B); opisthogastric shield with ten pairs of setae ***Parasitus consanguineus*** Oudemans & Voigts (p. 263)

– Posterior hypostomatic setae long and convoluted (Fig. 14G); sternal setae simple; opisthogastric shield with eight pairs of setae (Fig. 14B) 13

13 Podonotal shield over 450 μm long; endogynium as in figure 14C ***Parasitus fimetorum*** (Berlese) (p. 271)

– Podonotal shield less than 370 μm long; endogynium as in figure 7B ***Parasitus beta*** Oudemans & Voigts (p. 260)

14 Opisthonotal shield with usually 17–20 pairs of setae; podonotal shield with a pair of large conspicuous pores posterolaterally (Fig. 11G); opisthogastric shield with seven pairs of setae (Fig. 11H) . . . . ***Parasitus evertsi*** Oudemans (p. 269)

– Opisthonotal shield with more than 25 pairs of setae; podonotal shield without conspicuous pores posterolaterally; opisthogastric shield with eight or nine pairs of setae . . . 15

15 Opisthonotal shield of large proportions, completely covering the postero-dorsal region and extending ventrally, and bearing about 75 pairs of setae (Fig. 10L) ***Parasitus copridis*** Costa (p. 267)

– Opisthonotal shield of normal proportions, not extending to the ventral surface, and bearing approximately 30 pairs of setae (Fig. 21L) 16

16 Tectum with three subequal prongs (Fig. 18B, C); presternal shields absent; opisthogastric shield with eight pairs of setae of which the two postero-marginal pairs are stout and pilose (Fig. 18A); found exclusively on the seashore . ***Parasitus kempersi*** Oudemans (p. 280)

– Tectum with median prong long and blunt, lateral prongs shorter and denticulate (Fig. 21N); presternal shields small and triangular; opisthogastric shield with eight pairs of setae of which one postero-marginal pair is stout and pilose (Fig. 21M) ***Parasitus mustelarum*** Oudemans (p. 288)

17 Tectum trispinate, with lateral prongs well developed and their bases smooth (Figs 27D, 37C, 38J) 18

– Tectum otherwise (Figs 25D, 52N, 56J) 27

18 Opisthonotal shield with more than 35 pairs of setae 19

– Opisthonotal shield with less than 30 pairs of setae 21

19 Opisthonotal shield with about 60 pairs of setae; posterior margin of podonotal shield with four pairs of setae (Fig. 37A) . . . . . . ***Eugamasus cavernicola*** (Trägårdh) (p. 316)

– Opisthonotal shield with about 50 pairs of setae; posterior margin of podonotal shield with usually five pairs of setae (Fig. 36A) 20

20 Podonotal shield over 750 μm long; tectum as in figure 38J ***Eugamasus crassitarsis*** (Halbert) (p. 318)

– Podonotal shield less than 680 μm long; tectum as in figure 36C ***Eugamasus berlesei*** Willmann (p. 313)

21 Genital shield trispinate anteriorly, unusually long and extending to the level of coxae II (Fig. 40B) . . . . ***Porrhostaspis lunulata*** Müller (p. 320)

– Genital shield not trispinate, of normal proportions, not reaching beyond the midpoint of coxae III (Fig. 29B) 22

22 Opisthogastric shield with 8 pairs of setae (Fig. 15H); anterolateral seta on palp femur deeply bifurcate (Fig. 15L) . . . . ***Parasitus hyalinus*** (Willmann) (p. 277)

– Opisthogastric shield with nine or more pairs of setae; anterolateral seta on palp femur serrated (Figs 16N, 20E) 23

23 Peritreme not reaching coxa I; endogynium with medially directed hornlike processes (Fig. 16K); trochanter IV with small dorsal protuberance (Fig. 16P) ***Parasitus insignis*** (Holzmann) (p. 279)

– Peritreme extending to coxa I; endogynium without hornlike processes; trochanter IV without protuberance 24

24 Tectum with median prong shorter than laterals (Fig. 27D) 25

– Tectum with median prong stouter and longer than laterals (Fig. 20C) 26

25 Podonotal shield over 390 μm long; genital shield with a pair of lateral horns; sternal shield strongly sclerotized and usually indented posteriorly (Fig. 27C) ***Vulgarogamasus kraepelini*** (Berlese) (p. 297)

– Podonotal shield approximately 300 μm long; genital shield without lateral horns; sternal shield weakly sclerotized, not indented posteriorly ***Vulgarogamasus remberti*** (Oudemans) (p. 304)

26 Dorsal setae long, mostly reaching beyond the bases of the succeeding setae (Fig. 29A); podonotal shield less than 570 μm long; opisthogastric shield with 10 or 11 pairs of setae; genital shield with lateral horns (Fig. 29B); sterno-genital shields with weak reticulations ***Vulgarogamasus oudemansi*** (Berlese) (p. 300)

– Dorsal setae short, few reaching the bases of the succeeding setae (Fig. 20A); podonotal shield more than 630 μm long; opisthogastric shield with nine pairs of setae; genital shield without lateral horns; sterno-genital shields conspicuously ornamented (Fig. 20B) ***Parasitus loricatus*** (Wankel) (p. 283)

27 Opisthonotal shield pear shaped and considerably narrower than the podonotal shield which is tapered markedly behind setae *r3* (Fig. 33A); restricted to the seashore ***Vulgarogamasus trouessarti*** (Berlese) (p. 307)

– Opisthonotal shield not pear shaped and not conspicuously narrower than the podonotal (Figs 25A, 56H) 28

28 Leg II with spurs, especially on the femur and genu 29

– Leg II devoid of spurs 30

29 Femur II with two slender finger-like spurs and genu II with one (Fig. 52P); tectum trispinate with lateral margins deeply denticulate (Fig. 52N) ***Gamasodes bispinosus*** (Halbert) (p. 345)

– Femur, genu and tibia II each with one spur (Fig. 61K); tectum narrow with a trispinate tip (Fig. 61H) . . . . ***Poecilochirus davydovae*** sp. nov. (p. 358)

30 Opisthonotal shield with approximately 40 pairs of setae; postanal seta considerably longer than the paranals (Fig. 56I) 31

– Opisthonotal shield with less than 30 pairs of setae; anal setae subequal (Fig. 23B) . . . 32

31 Podonotal shield more than 650 μm long; opisthonotal shield more than 850 μm long; tectum finely tapered anteriorly with angular serrated margins (Fig. 56J) ***Poecilochirus carabi*** G. & R. Canestrini (p. 350)

– Podonotal shield less than 550 μm long; opisthonotal shield less than 600 μm long; tectum tapering with its apex flanked by a pair of small prongs (Fig. 59C) ***Poecilochirus austroasiaticus*** Vitzthum (p. 355)

32 Large species, podonotal shield more than 1200 μm long, opisthonotal shield more than 800 μm long; restricted to the seashore . ***Vulgarogamasus immanis*** (Berlese) (p. 292)

– Small species, podonotal and opisthonotal shields each less than 400 μm long ***Vulgarogamasus burchanensis*** (Oudemans) (p. 290)

Genus *PARASITUS* Latreille

Parasitus Latreille, 1795. *Magazin encycl.* **4** (13): 19.
Carpais Latreille, 1796. (In part). *Précis des caractères génériques des insectes disposés dans un ordre naturel.* Abrive: 184.
Gamasus Latreille, 1802. *Histoire naturelle, générale et particulière des crustacés et des insectes.* Paris, **3:** 64.
Coleogamasus Tichomirov, 1969. *Zool. Zh.* **48:** 1470.

TYPE SPECIES. *Acarus coleoptratorum* Linnaeus, 1758.

Dorsal shield of male entire, with transverse suture; female and deutonymph with separate podonotal and opisthonotal shields. Setae *z5* of dorsal hexagon usually markedly different in form from *j5* and *j6*. Tritosternum of male absent or variously modified, or if biramous, then base closely associated with genital orifice; tritosternum of female and deutonymph normal. Junction between sternal and metasternal shields of female oblique. Genital shield of female triangular or subtriangular. Opisthogaster with rarely more than 30 pairs of setae. Seta *al* of palp femur bifid or with one or more distinct slender processes; setae al_1 and al_2 of palp genu entire, spatulate or setiform. Male chelicerae symmetrical. Corniculi short, entire or bifid, rarely otherwise modified. Legs of deutonymph and female without spurs, at most with strong setae; only leg II of male spurred. Lobes of pulvilli normal, rounded.

Parasitus coleoptratorum (Linnaeus)
(Figs 3A–M; 4A–F)

Acarus coleoptratorum Linnaeus, 1758: 618.
Gamasus (Gamasus) coleoptratorum (Linn.) sensu Latreille, Berlese, 1906: 155.
Gamasus coleoptratorum: Hull, 1917: 103. Non Berlese, 1892*b*: Fasc. 69, T.7 = *Gamasus distinctus* Berl., 1904*a*.
Parasitus coleoptratorum: Oudemans, 1908: 28. Costa, 1963: 27, Micherdzinski, 1969: 393. Karg, 1971: 446. Evans & Till, 1979: 210.
Eugamasus celer (C. L. Koch, 1835) sensu Holzmann, 1969: 8.
Parasitus (Coleogamasus) celer: Tichomirov, 1969: 1476. Bregetova *et al.,* 1977: 85, 89.

DEUTONYMPH. The reticulated dorsal shields are strongly sclerotized and generally rich yellow to brown in colour. The podonotal shield (600–754 μm long × 700–754 μm wide) bears 20 pairs of setae of which *j1, j4, z5* and *r3* are long, stout and pilose distally, the remainder being very short and simple, with *s2* situated off the shield. Setae *j1* and *z1* are situated on a prominent transverse granular band (Fig. 3A). The opisthonotal shield (370–415 μm long × 620–672 μm wide) bears 16 pairs of setae of which 15 pairs are short and simple and *Z3* are long (*c.* 125 μm), stout and pilose distally. The surrounding membrane bears dorsally on each side between 40 and 50 very short setae.

The tritosternum has a narrow base and pilose laciniae. The sternal shield (384–410 μm long) is reticulated with a pale anterior transverse strip, the setae normally appear simple, *st.* I are occasionally finely pilose. The presternal shields are frequently absent or barely discernible, but when present they are small (Fig. 3B). The oval anal shield bears the normal three setae, the paranals being the longest. The stigma is situated opposite the posterior margin of coxa III and the peritreme extends anteriorly to the level of coxa I. The opisthogastric setae are all simple.

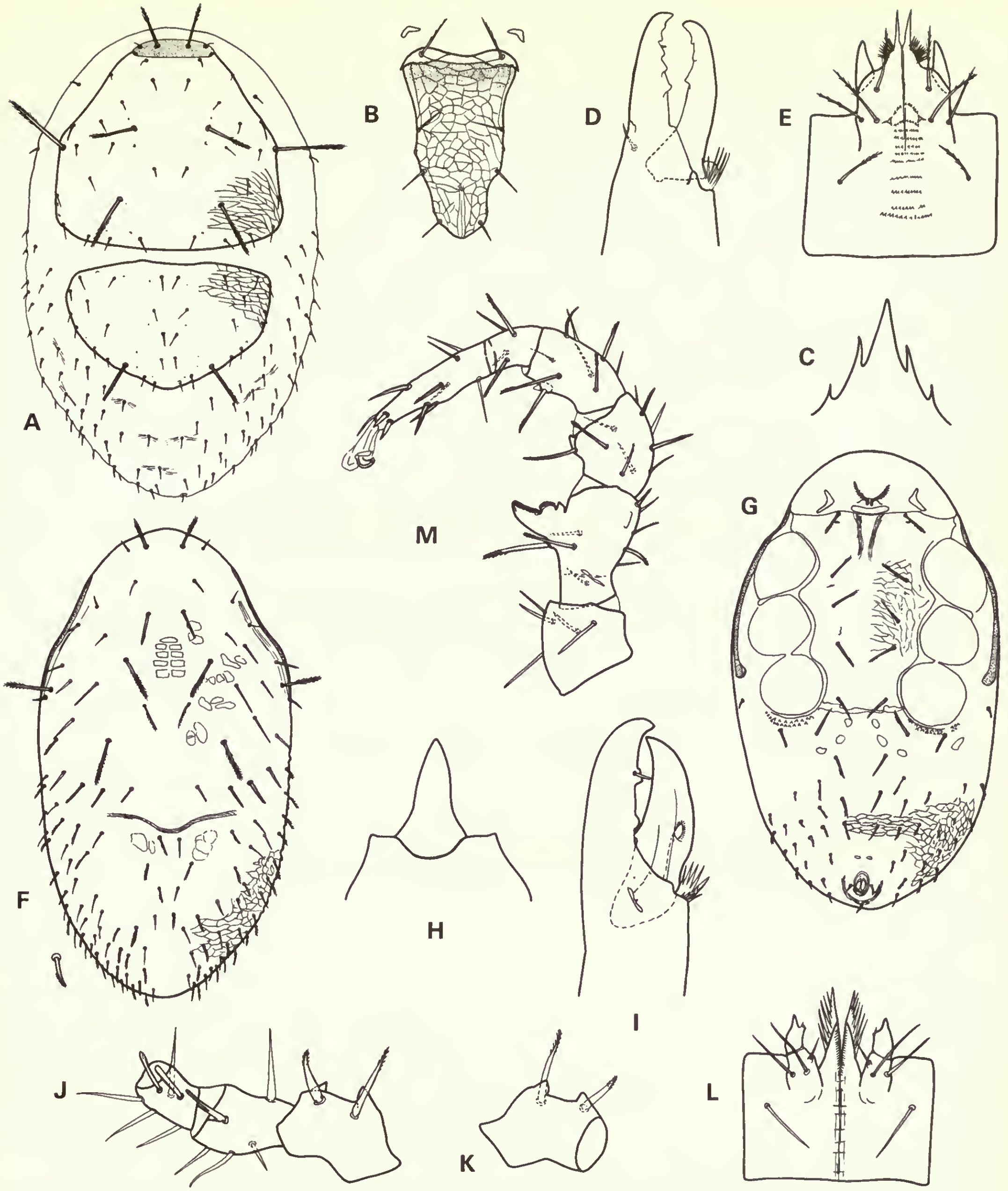

Fig. 3 *Parasitus coleoptratorum* (L.), **deutonymph** – A dorsum; B sternal shield; C tectum; D chelicera; E venter of gnathosoma: **male** – F dorsum; G venter; H tectum; I chelicera; J palp trochanter, femur and genu; K palp trochanter; L venter of gnathosoma; M left leg II. .

The five-pointed tectum appears to show very little variation (Fig. 3C). The chelicera is as in figure 3D, whilst the anterolateral setae of the palp femur and genu are as in the female (Fig. 4E). The corniculi and venter of the gnathosoma are as in figure 3E. All legs bear a number of finely pilose setae, mainly on the proximal segments, whilst on legs III and IV the setae are markedly stouter than on legs I and II. The pulvilli are normal.

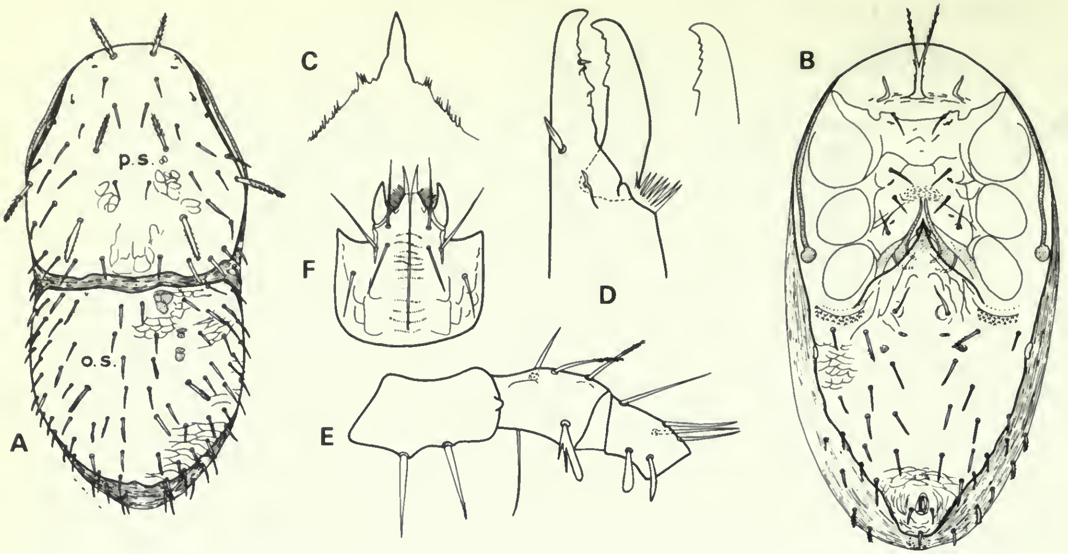

Fig. 4 *Parasitus coleoptratorum* (L.), **female** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma. *p.s.*, podonotal shield, *o.s.*, opisthonotal shield.

MALE. The dorsal shield (1260–1320 μm long × 720–780 μm wide) is entire with a transverse undulating suture. It is mainly reticulated, especially around the margins, whilst medially are isolated granular areas (Fig. 3F). The podonotal region bears about 24 pairs of setae, in the specimen figured the left *z3* is lacking. Setae *j1, j4, z5* and *r3* are the longest and are stout and finely pilose. Others, for example *j3* and *s5*, are also stouter than the remainder which are predominately short, curved and blade-like as shown in the inset. The opisthonotal region bears about 37–45 setae on each side, mainly located in the marginal area.

The tritosternum comprises two pilose laciniae which arise from a slight protuberance anterior to the genital lamina (Fig. 3G). The sternogenital setae are simple, whilst the paired paranal and single postanal setae are stout, slightly curved and of similar length to the majority of the posterior opisthogastric setae. The median and anterior opisthogastric setae approach the length of the sternogenitals. The stigma is opposite the posterior margin of coxa III and the peritreme extends anteriorly to the level of coxa I. A double row of small teeth is situated immediately posterior to coxa IV.

The tectum, which appears to show little variation, comprises a tapered prominence arising from a broad squarish base (Fig. 3H). The chelicera is as in figure 3I: the movable digit is broad and curved with a single tooth midway, whilst the fixed digit bears two teeth. The palp trochanter, femur and genu are shown in figure 3J. The trochanter bears two prominent tooth-like protuberances ventrally and the anterior seta is stout (Figs 3J, K). The anterolateral seta on the femur is trispinate whilst the two anterolaterals on the genu are spatulate. The venter of the gnathosoma is as in figure 3L. The corniculi, which are stalked and broad at their bases, bear an excrescence midway on the inner margin. The anterior hypostomatic setae are short and extremely slender whilst the posterior hypostomatic and palpcoxal setae are stout and long. Between eight and 12 rows of hypognathal denticles are normally apparent. Leg II is shown in detail in figure 3M. Many of the leg setae are very finely pilose at their tips and often along one margin.

FEMALE. The podonotal shield (720–792 μm long × 660–768 μm wide) bears 21 pairs of setae of which *j1, j4, z5* and *r3* are longer and stouter than the remainder and are finely pilose (Fig. 4A). As in the male, the shorter setae are mainly curved and pilose distally. The opisthonotal shield (650–700 μm long × 708–816 μm wide) bears approximately 34–36 pairs of setae of which *Z3* are the stoutest. The arrangement of setae on this shield is apparently symmetrical, but it is not easy to be certain if any of the marginal setae have been detached due to the crenate border concealing the setal bases. The small area of interscutal membrane posterior to the opisthonotal shield bears only about five pairs of setae.

The tritosternum has a narrow base and pilose laciniae. It is flanked by a pair of L-shaped presternal shields (Fig. 4B). The sternal and metasternal shields are granular and the setae are simple. The genital shield is sharply pointed anteriorly. The opisthogastric shield tapers somewhat irregularly and bears between 10 and 12 pairs of setae, normally arranged symmetrically, but varying in number depending on whether or not the laterals are on or off the shield. The three anal setae are of approximately equal length. The lateral membrane bears few setae. The stigma is situated opposite the posterior margin of coxa III and the peritreme extends anteriorly to the level of coxa I.

The tectum has a single strong tapered prominence similar to the male, but this arises from a sharply toothed tapered base (Fig. 4C). The chelicera is as in figure 4D, with the dentition of the movable digit of the second chelicera of the same specimen inset. The palp trochanter, genu and femur are shown in figure 4E and the venter of the gnathosoma in figure 4F. Many of the leg setae are finely pilose at their tips and along one margin. No characteristic setal formations are present.

MATERIAL EXAMINED. 218 samples – 9 PNN, *c.* 1650 DNN, 53 ♂♂, 67 ♀♀.

ENGLAND: Isles of Scilly, Cornwall (mainland), Devon, Dorset, Gloucestershire, Hampshire, Isle of Wight, Surrey, Sussex, Kent, London, Essex, Middlesex, Hertfordshire, Buckinghamshire, Cambridgeshire, Norfolk, Huntingdonshire, Worcestershire, Leicestershire, Lincolnshire, Derbyshire, Cheshire, Lancashire, Manchester, Westmorland, Cumberland, Yorkshire, Northumberland, Durham.

WALES: Pembrokeshire, Radnorshire, Cardiganshire, Montgomeryshire, Merionethshire, Caernarvonshire, Anglesey.

SCOTLAND: Roxburghshire/Midlothian borders, Dunbartonshire, Kirkudbrightshire, Argyllshire, Angus, Outer Hebrides, Inner Hebrides, Shetland, Fair Isle.

IRELAND: Cork, Kildare, Westmeath, Meath, Clare, Galway, Sligo.

Parasitus coleoptratorum is possibly the most common European member of the genus and is distributed throughout the British Isles. The deutonymphs are well known as paraphages of Coleoptera (Hull, 1918, Hyatt, 1959) and of the 218 samples examined in the present work 107 are from beetles of the following genera: *Geotrupes, Onthophagus, Typhaeus, Aphodius, Nicrophorus* and *Hister.* The adults are found much less frequently than the deutonymphs and they are confined (occasionally in association with deutonymphs) mainly to compost, manure (Hull, 1918) and rich humus, including rotting seaweed, as well as the nests of small mammals and occasionally birds. Only one instance of adults and deutonymphs from a beetle has come to my notice, viz. 3 DNN, 1 ♂, 1 ♀ ex *Geotrupes spiniger* (Marsham), Heddon-on-the-Wall, Newcastle-upon-Tyne, 2 October 1969, coll. M. L. Luff. The only specimen examined from a non-coleopterous insect is a single deutonymph in the Hull Collection from a caterpillar of the puss-moth *Cerura vinula* (L.), Bowden, Cheshire, 4 August 1917, coll. T. A. Coward. A single deutonymph has been examined from bat dung, Bryanston, Devon, 1977.

DISTRIBUTION. Previous British records are from the Tyne Province ('common everywhere', Hull, 1918), Co. Mayo and Co. Dublin (Halbert, 1915, 1920), the Inner Hebrides (Bertram, 1939), Hertfordshire (Hyatt, 1956), Isles of Scilly (Evans, 1957*b*), Dorset and the Isles of Scilly (Hyatt, 1959), Devon (Mean-Briggs & Hughes, 1966) and Cumberland (Turk, 1972). Turk (1967) records this species from caves without giving a locality and specimens have not been examined by me. Hazelton (1967*a*) records it from a cave in Somerset and from a mine in Cumberland, the latter being the same record as given by Turk (1972).

It is recorded from Iceland (Sellnick, 1928, 1940), the Faeroes (Trägårdh, 1931), Finland (Nordberg, 1936, Willmann, 1938*c*), Holland (Oudemans, 1896, 1900, 1902*b*, 1903*a* 1905*b*, 1908), Belgium (van Daele & Heungens, 1974, 1975), Germany (Koch, 1835, Voigts & Oudemans, 1904, 1905, Vitzthum, 1927, 1930*a*, Karg, 1971), Austria (Franz, 1943, Leitner, 1946), Switzerland (Schweizer, 1922, 1949, 1961), Italy (Berlese, 1906, 1913, Valle, 1955), Hungary (Valle, 1955), Czechoslovakia (Müller, 1860, Willmann, 1954), Poland (Schweizer, 1926, Willmann, 1956, Micherdzinski, 1969), Western Siberia (Davydova, 1969, 1976), and also from Israel (Shulov, 1957, Costa, 1963, 1966) and Chile (Berlese & Leonardi, 1902).

Parasitus beta Oudemans and Voigts

(Figs 5A–F; 6A–G; 7A–F)

Parasitus beta Oudemans & Voigts, 1904 in Voigts & Oudemans, 1904: 652; 1905: 219. Type examined.

Parasitus eta Oudemans & Voigts, 1904 sensu Karg, 1965: 303, fig. 59*b*, ♀ only; 1971: 425, ♀ only. *Parasitus eta* Ouds. & Vgts., 1904 (DN only described) = *P. fimetorum* Berlese, 1904, *q.v.*

Several species have been described, most as deutonymphs only, which show a close resemblance to *Parasitus fimetorum* Berlese, 1904. Most of these fall within the size range examined for that species, but some are considerably smaller. The main similarities are, in the deutonymph, the dorsal chaetotaxy, and in the female, the contorted posterior hypostomatic setae and the close proximity to each other of sternal setae I and the shape of the genital shield. However, as far as I can ascertain following comparison with the types of several of these species, viz. *Parasitus eta, beta* and *alpha,* all Oudemans & Voigts, 1904, and *Gamasus distinctus* Berlese, 1904* and by reference to the figures of *Parasitus nolli* Karg, 1965, and *Gamasus neglectus* Berlese, 1904, the only species which has dorsal setae *s5* clearly stout like *z5* (especially in the deutonymph) is *Parasitus beta.*

The 65 deutonymphs, 4 males and 8 females that I am assigning to this taxon are from 15 samples, several of which contained no other *Parasitus,* whilst the remainder contained *Parasitus* species that could not be confused with the present one.

DEUTONYMPH. The dorsal shields are generally weakly sclerotized and entirely reticulated (Fig. 5A). The podonotal shield (300–336 μm long × 290–384 μm wide) bears 20 pairs of setae, *s2* being situated off the shield. Setae *j1, j4, z5, s5, s6* and *r3* are stouter than the remaining setae which are very fine. The longest and stoutest, *r3* (*c.* 100 μm), are also finely pilose. The opisthonotal shield (190–240 μm long × 250–360 μm wide) bears 15 pairs of setae of which three, *J5, Z3* and *S4,* are clearly stouter than the other marginal setae. The inner setae are very fine and slender. The setae on the posterior membrane are intermediate in thickness.

The tritosternum has a narrow base and pilose laciniae. The presternal shields are weakly sclerotized (Fig. 5B). The sternal shield (204–240 μm long) is finely reticulated and the setae are simple. The reticulated anal shield is oval and the three setae are simple. The opisthogastric setae are simple and, as on the dorsum, the median setae are the finest. The peritreme extends to coxa I.

The tectum is trispinate with the centre prong usually giving the appearance of being damaged distally (Fig. 5C). The chelicera is as in figure 5D: the movable digit measures *c.* 45 μm. The chaetotaxy of the palp trochanter, femur and genu is shown in figure 5E, and the venter of the gnathosoma in figure 5F. The leg setae are simple and all of similar form. Tarsus IV bears dorsally a conspicuous erect seta *c.* 120 μm in length.

MALE. The dorsum (580–600 μm long × 340 μm wide) is entire and with a transverse suture (Fig. 6A). It is completely reticulated but not strongly sclerotized. The podonotal region bears 21 pairs of setae of which *j1, j4, z5, s5* and *r3* are the stoutest. The remainder are slender. The opisthonotal region bears approximately 30 pairs of setae of which *Z1* and *Z3* are the stoutest and those towards the margins are almost as stout, whilst *J1–J4* are slender.

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*Cited by Karg (1971: 447) as *Parasitus distructus* (Berlese).

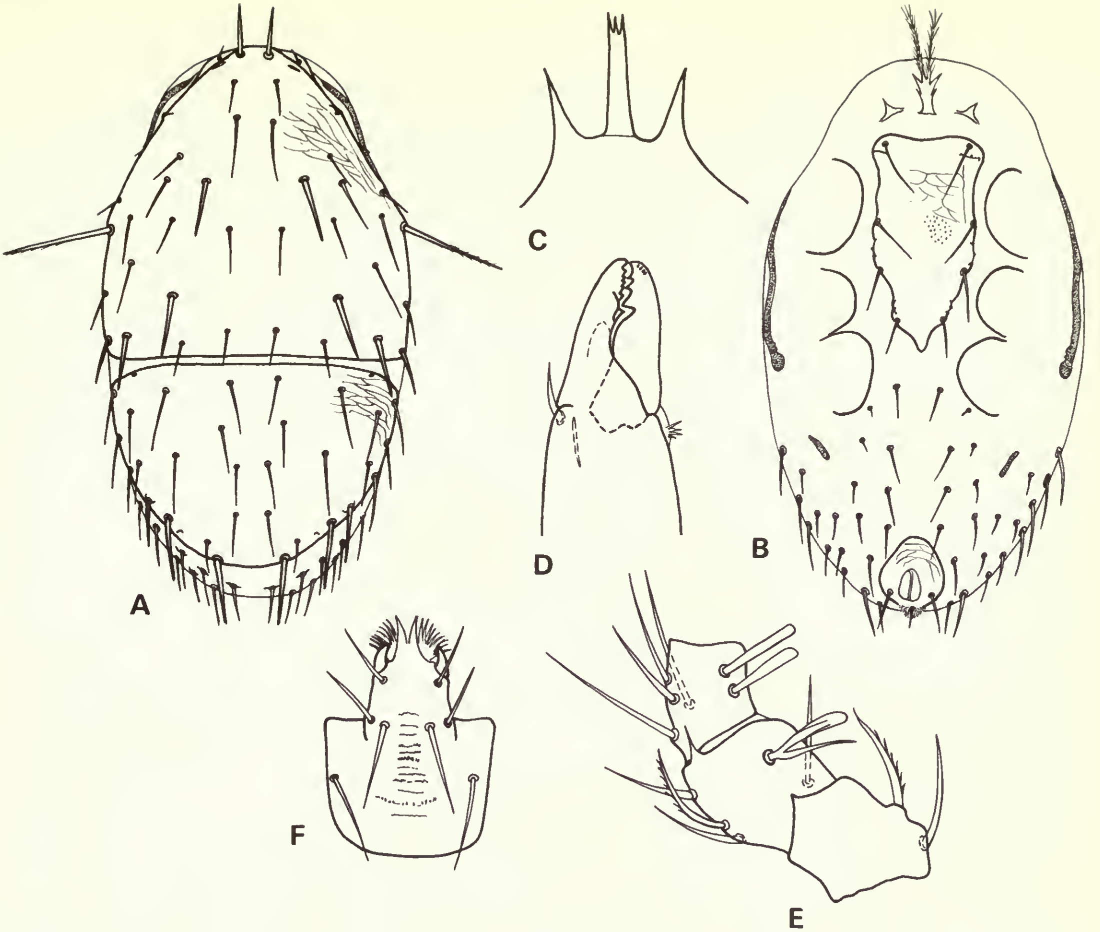

Fig. 5 *Parasitus beta* Oudemans & Voigts, **deutonymph** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma.

The tritosternum, which measures *c.* 45 μm in total length, has very fine slender laciniae and a rudimentary base (Fig. 6B). The ventral sclerotization and chaetotaxy are little different from those of *P. fimetorum,* although the more posterior setae are shorter. The peritreme extends to coxa I.

The tectum is trispinate, the centre spine being slightly the longest (Fig. 6C). The chelicera is shown in figure 6D, and the palp trochanter, femur and genu in figure 6E. The corniculi are short, pointed and strongly stalked and the gnathosomal setae are simple (Fig. 6F). The leg setae all appear to be simple and are generally rather strong relative to the overall weakness of sclerotization. Leg II is shown in detail in figure 6G. In one specimen from Ireland the right leg II lacks all spurs.

FEMALE. The podonotal shield (350–360 μm long × 370 μm wide) is finely reticulated and bears 21 pairs of setae of which *j1, j4, z5* and *r3* (*c.* 100 μm) are longer and stouter than the remainder and are finely pilose (Fig. 7A). Seta *s5* is also stout but not long. The opisthonotal shield (330–350 μm long × 360–370 μm wide) is also reticulated and bears 26 pairs of setae of which *Z1, Z3* and *J5* are the stoutest and are finely pilose at least distally. The lateral setae are generally stouter than *J1–J4.*

The tritosternum has a narrow base and pilose laciniae. It is flanked by weakly sclerotized presternal shields (Fig. 7B). The sternal shield is particularly weakly sclerotized. The sternal setae are stouter than the metasternals and genitals. The genital shield is strongly pointed

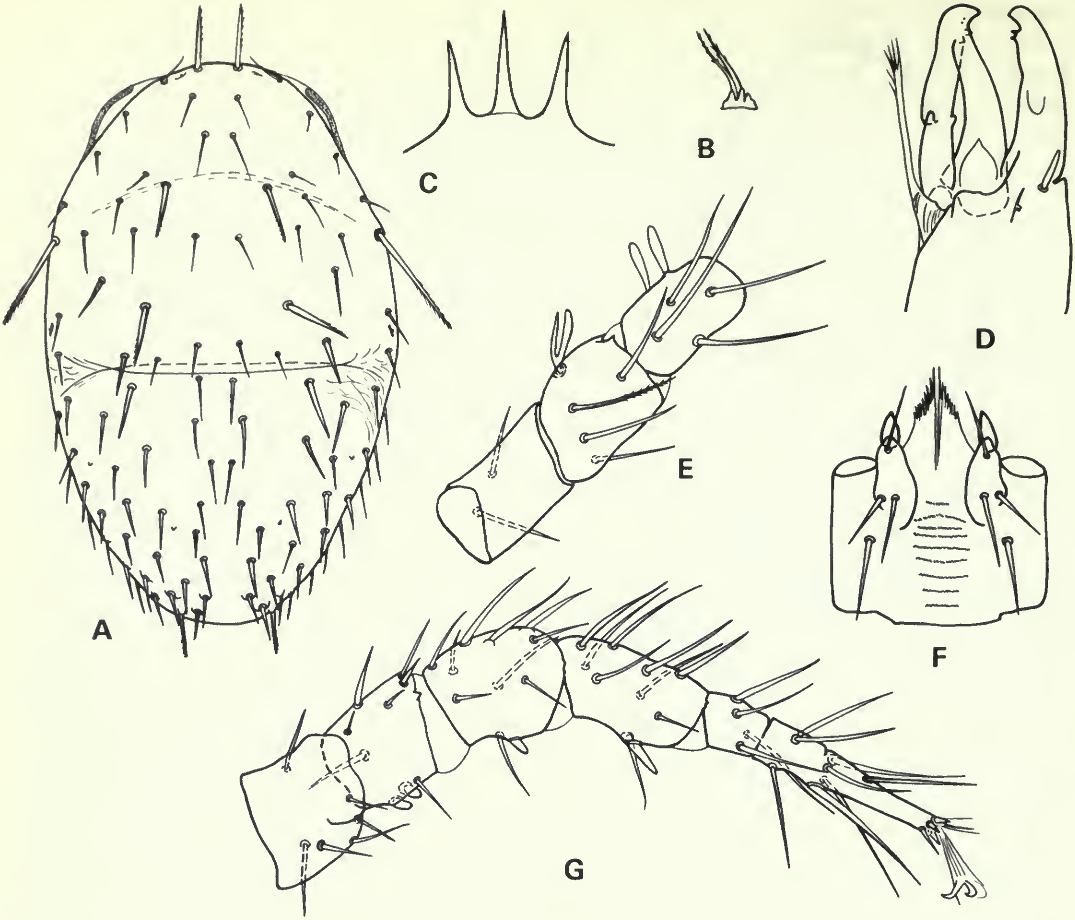

Fig. 6 *Parasitus beta* Oudemans & Voigts, **male** – A dorsum; B tritosternum; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma; G leg II.

anteriorly, whilst posteriorly it merges with the weakly sclerotized but reticulated opisthogastric shield. The endogynium shows a mushroom-shaped process. The lateral margins of the opisthogastric shield are sometimes irregularly formed and of the eight pairs of setae, two marginal pairs are conspicuously long and stout. The anal setae are simple. The peritreme extends to coxa I.

The tectum is trispinate with the centre prong multifid (Fig. 7C). The chelicera is shown in figure 7D, and the chaetotaxy of the palp trochanter, femur and genu in figure 7E. The corniculi are short and tapered and the posterior hypostomatic setae are long and contorted (Fig. 7F). The leg setae are mainly long and fine and all appear to be simple.

MATERIAL EXAMINED. 15 samples – 65 DNN, 4 ♂♂, 8 ♀♀.

ENGLAND: Cornwall, Somerset, Gloucestershire, Surrey, Kent, Cambridgeshire, Suffolk, Northamptonshire, Leicestershire.
SCOTLAND: Isle of Muck.
IRELAND: Kildare, Westmeath.

Most samples are from grassland, although a female and four deutonymphs from Cornwall are from dried seaweed, seven deutonymphs from Kent are from *Aphodius* sp. (Coleoptera) and a single deutonymph from the Isle of Muck is from *Apodemus sylvaticus* (L.).

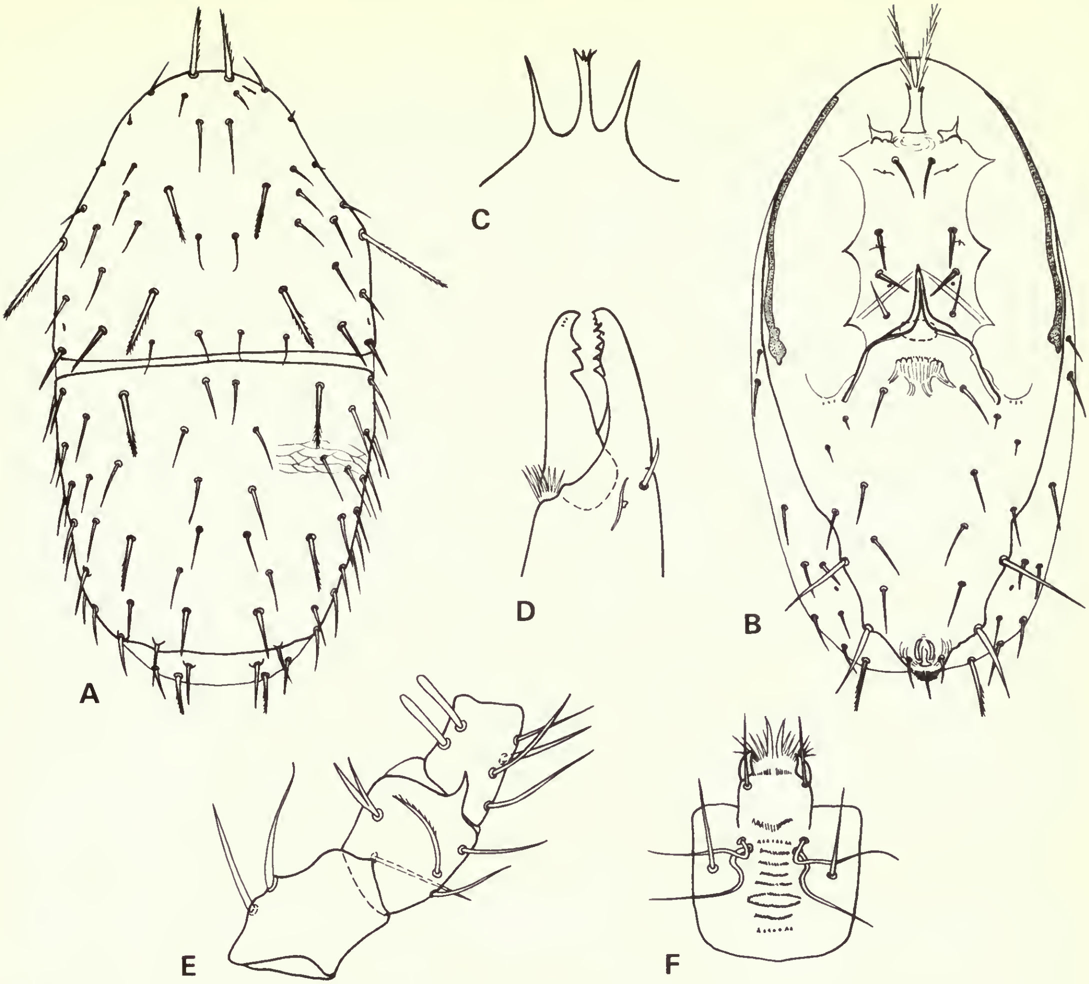

Fig. 7 *Parasitus beta* Oudemans & Voigts, **female** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma.

Distribution. This species has not been recorded from the British Isles. Previous records are from Germany (Voigts & Oudemans, 1904, 1905, Karg, 1965, 1971, Michertzinski, 1969).

Parasitus consanguineus Oudemans & Voigts
(Figs 8A–O; 9A–F)

Parasitus consanguineus Oudemans & Voigts, 1904 in Voigts & Oudemans, 1904: 651. Costa, 1961: 265. Micherdzinski, 1969: 466. Karg, 1971: 446.
Parasitus (Coleogamasus) consanguineus: Tichomirov, 1969: 1476. Bregetova *et al.*, 1977: 88, 91.
Parasitus setosus Oudemans & Voigts, 1904 in Voigts & Oudemans, 1904: 653. Costa, 1961: 265.
Parasitus thoni (Berlese) sensu Sellnick, 1931: 743. Costa, 1961: 265.
Parasitus jugulatus Schweizer, 1949: 10; 1961: 15. Costa, 1961: 265. Type examined.
Eugamasus consanguineus: Holzmann, 1969: 16.

The synonymy given above is that generally followed. A number of additional species have been described* that share in the females the forked sternal seta I, and in the deutonymphs the characteristic '*jugulatus*' appearance of the sternal shield in which the sclerotization of

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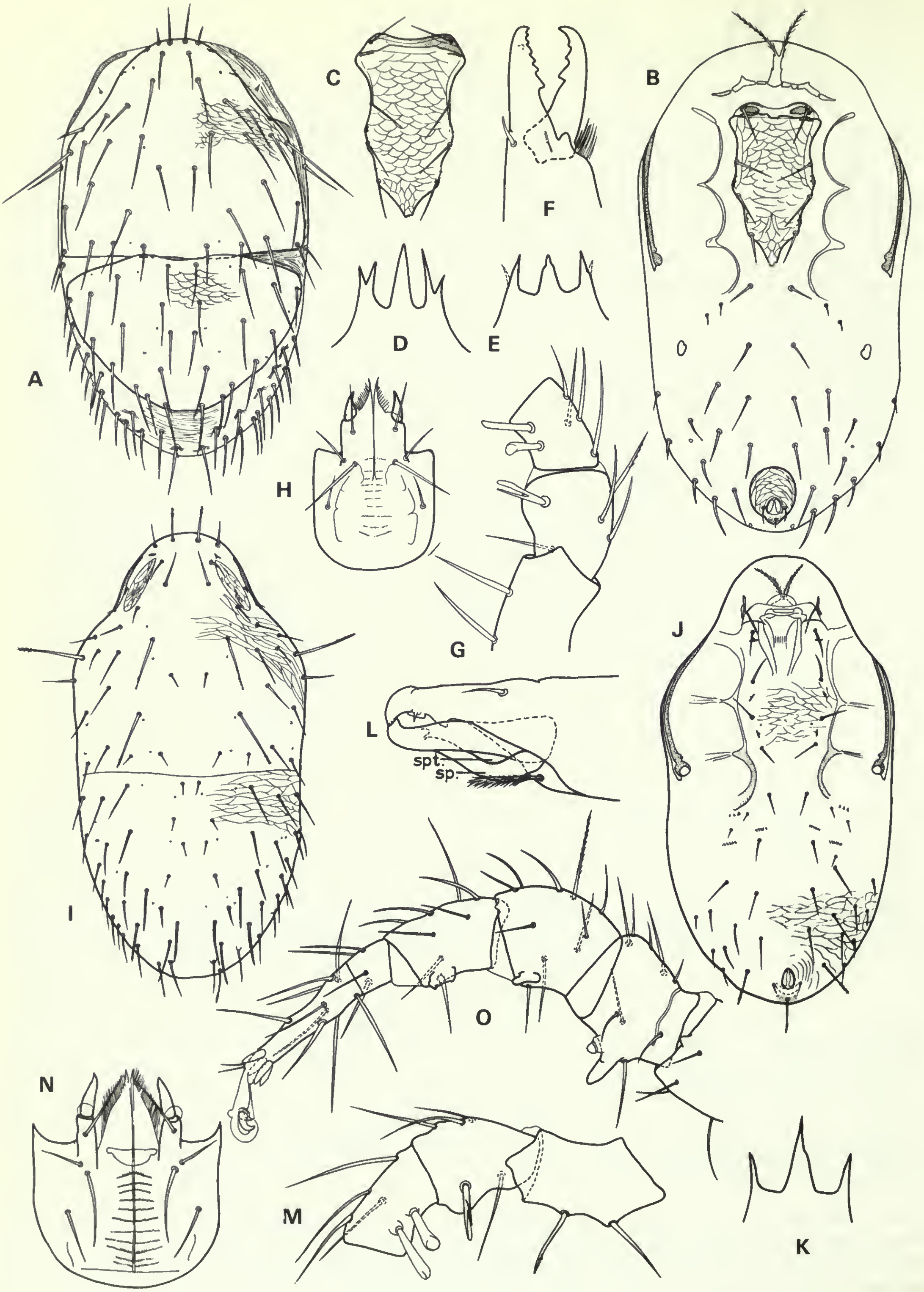
**Gamasus (G.) mammillatus* Berlese, 1904, *Eugamasus numerus* Karg, 1965, *Eugamasus eustructurus* Holzmann, 1969 and *Parasitus tichomirovi* Davydova, 1969.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the anterior region gives the appearance, in many specimens, of having separate *jugular* shields (Fig. 8B). The deutonymphs also have the lateral prongs of the tectum bifid in varying degrees (Figs 8D & E). Recent comments by Karg (1972) and Costa (1975) have only served to emphasize the need for specialized collecting and laboratory rearing of complete life-cycles as has been done, for example, on *Parasitus copridis* Costa (Costa, 1964).

Deutonymph. The dorsal shields are strongly sclerotized and in the majority of specimens are of a dull brown colour, conspicuous in both fresh spirit-preserved material and in permanent mounts. The podonotal shield (312–432 μm long × 312–456 μm wide) bears 20 pairs of simple setae, *s2* being situated off the shield (Fig. 8A). There are no stout setae. The opisthonotal shield (204–300 μm long × 312–444 μm wide) bears 13 pairs of simple setae. The setae on the posterior interscutal membrane are similar to those of the opisthonotal shield.

The tritosternum has a narrow base and pilose laciniae. It is flanked by conspicuously long fragmented presternal shields. The sternal shield (240–276 μm long) is strongly sclerotized and completely reticulated and bears four pairs of simple setae. Anteriorly the sclerotization is frequently fragmentary with sternal setae I giving the appearance of being on separate shields or *jugularia* as in figure 8B. This condition appears to be extremely variable even within specimens from one sample, and an extreme example without signs of fragmentation, although with a weakly sclerotized anterior strip, is shown in figure 8C. The circular to oval anal shield is entirely reticulated and the anal setae are short and simple. The finely granular peritreme extends to the level of coxa I. The opisthogastric membrane bears approximately 16 pairs of simple setae which are not always symmetrically arranged. The metapodal shields are strongly sclerotized and may be almost square or circular.

The tectum is trispinate with the lateral prongs normally bifurcate (Fig. 8D), but some irregularity does occur (Fig. 8E). The chelicera is shown in figure 8F. Little variation has been noticed in the dentition. The chaetotaxy of the palp trochanter, femur and genu is as in figure 8G and the corniculi and gnathosomal setae in figure 8H. Ten rows of hypognathal denticles are normally clearly visible. All setae on the legs are simple although degrees of stoutness occur.

Male. The dorsal shield (840–953 μm long × 456–477 μm wide) is entire with a transverse median suture (Fig. 8I). It is entirely reticulate and well sclerotized. The podonotal region bears 22 pairs of setae of which *j1, j4, z5* and *r3* are conspicuously stouter and generally finely pilose distally – at least on one margin. The opisthonotal region bears usually 26 or 27 pairs of setae of which few only show occasional pilosity. Setae *J1–J4* are short and noticeably finer than the remainder.

The tritosternum bears finely pilose laciniae but the base is very short and broad (Fig. 8J). The genital lamina protrudes anteriorly from the holoventral shield whilst the presternal shields are generally obscure or lacking. The sternogenital setae are fine and simple. There are approximately 15 pairs of opisthogastric setae, occasionally these are not paired, and one or two pairs in the anal region are finely pilose distally. The paranal setae are short and simple whilst the postanal is long and finely pilose distally. The peritreme extends to the anterior level of coxa I.

The tectum is trispinate but has the centre prong sometimes irregular (Fig. 8K). The chelicera is shown in figure 8L: the tips of the chelae are strongly rounded whilst the spermatodactyl curves strongly away from the movable digit basally. The palp trochanter, femur and genu are shown in figure 8M. The corniculi are strongly stalked and are curved at their tips, whilst the gnathosomal setae are simple (Fig. 8N). Eleven or more rows of hypognathal denticles are discernible. The leg setae are mainly simple, although some

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Fig. 8 *Parasitus consanguineus* Oudemans & Voigts, **deutonymph** – A dorsum; B venter; C variant form of sternal shield; D, E tectum; F chelicera; G palp trochanter, femur and genu; H venter of gnathosoma: **male** – I dorsum; J venter; K tectum; L chelicera; M palp trochanter, femur and genu; N venter of gnathosoma; O leg II.

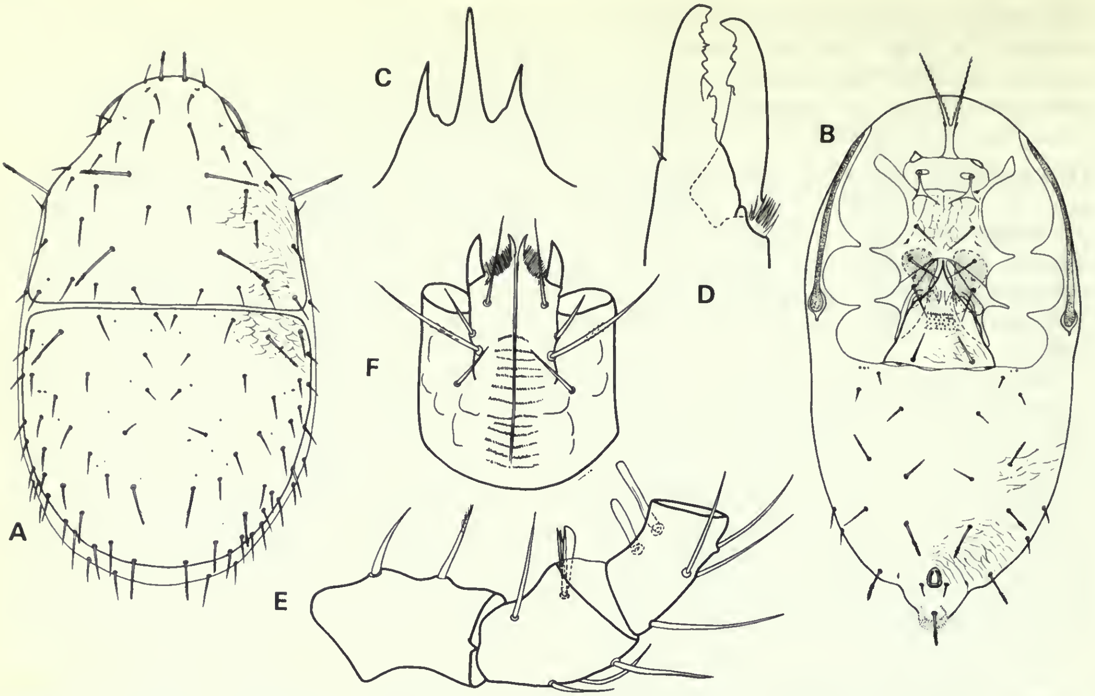


Fig. 9 *Parasitus consanguineus* Oudemans & Voigts, **female** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma.

dorsals are erect and usually finely pilose at least on one margin. Leg II is shown in figure 8O. The femoral spur is smooth in outline and the auxiliary is short and domed.

FEMALE. The podonotal shield (518–552 μm long × 528–624 μm wide) bears 21 pairs of setae of which *j1, j4, z5* and *r3* are conspicuously longer and stouter than the remainder and are more clearly very finely pilose distally (Fig. 9A). The opisthonotal shield (591–600 μm long × 546–636 μm wide) bears at least 31 or 32 pairs of setae of which the stoutest are finely pilose distally, and *J1–J4* are, as in the male, short and finer than the remainder. The posterior interscutal membrane bears few setae.

The tritosternum has pilose laciniae and a narrow base. It is flanked by rudimentary presternal shields (Fig. 9B). The sternal shield is rather weakly sclerotized anteriorly and sternal setae I, which are forked distally, arise from small plates situated in the weakly sclerotized area. Sternal setae II–IV are simple and of equal length, but *st.* IV (the metasternals) are slightly more slender. The genital shield is tall and triangular with a pointed apex whilst the setae are simple. Internally, the most conspicuous part of the endogynium is the rows of teeth across the centre of the genital shield. The opisthogastric shield is well sclerotized and bears 10 pairs of setae of which four pairs are stout with some pilosity distally. The paranal setae are short (*c.* 37 μm) and simple whilst the postanal is long (*c.* 80–95 μm) and pilose distally. The peritreme extends anteriorly to beyond coxa I.

The tectum (Fig. 9C) is strong and broadly trispinate with the centre prong longest. The chelicera (Fig. 9D) bears three teeth on the movable digit and four on the fixed. The palp trochanter, femur and genu (Fig. 9E) are as in the male. The corniculi are smooth and the gnathosomal setae are simple with the external posterior rostrals almost twice as long as the others. There are 13 rows of more or less distinct hypognathal denticles (Fig. 9F). The leg setae are almost all simple although some show traces of fine pilosity. Genu II and genu and tarsus IV each bear one stout dorsal seta which is clearly but finely pilose distally.

MATERIAL EXAMINED. 47 samples – 3 PNN, 74 DNN, 12 ♂♂, 22 ♀♀.

ENGLAND: Isles of Scilly, Dorset, Hampshire, Sussex, Surrey, Kent, London, Middlesex,

Berkshire, Buckinghamshire, Essex, Norfolk, Derbyshire, Nottinghamshire, Manchester, Lancashire, Yorkshire.
WALES: Anglesey.
SCOTLAND: Glasgow, Iona, Mull, Orkney.
IRELAND: Cork.

Most samples were obtained from decaying vegetable matter, compost, or from manure with straw and a few were from surface leaf-litter. One sample was obtained from spent hops, another from grain spillage and two from seashore debris. Also one, Manchester, 28 August 1936 on *Aphodius rufipes* (L.) (Coleoptera), one, no data, J. E. Hull Collection, from *Geotrupes* sp. (Col.), and one from Norfolk, 1969, on *Bombus pascuorum* (Scopoli) (Hymenoptera), coll. Miss S. P. Greenwood. A single deutonymph from a starling's nest in a sand martin's burrow, Ballycroneen Strand, Co. Cork, 3 June 1964, coll. A. J. M. Claassens, is the only record from Ireland.

DISTRIBUTION. Only previously recorded in the British Isles by Hull (1918) from Northumberland and Miles (1955) from Cardiganshire, this species is never found abundantly.

It is recorded from Iceland (Sellnick, 1940), Sweden (Sellnick, 1958), Holland (Oudemans Collection), Belgium (van Daele & Heungens, 1974, 1975), Germany (Voigts & Oudemans, 1904, Karg, 1965, 1971, Holzmann, 1969, Micherdzinski, 1969), U.S.S.R. (Pinchuk, 1976), Ukraine (Pirjanik, 1962), Western Siberia (Davydova, 1969, 1976), Greece (Sellnick, 1931) and Israel (Costa, 1961, 1966). Its habitats are mainly dung and compost with additionally arable and meadow land.

Parasitus copridis Costa
(Fig. 10A–P)

Parasitus copridis Costa, 1963: 29; 1964: 209. Micherdzinski, 1969: 417. Davydova, 1976: 89.
Parasitus (Coleogamasus) copridis: Tichomirov, 1969: 1476. Bregetova *et al.*, 1977: 83, 89.

DEUTONYMPH. The podonotal shield (444–502 μm long × 504–564 μm wide) is finely reticulated and bears 20 pairs of setae, *s2* being situated off the shield. The relative lengths of the setae are shown in figure 10A. The opisthonotal shield (300–336 μm long × 456–540 μm wide) is also finely reticulated. It bears 14 pairs of setae of which only *Z3,* situated on the margin, are long (*c.* 260 μm) (Costa, 1963 gives 390 μm), stout and finely pilose. The remaining setae are fine and short (*c.* 47 μm maximum). The interscutal membrane bears short, simple setae only.

The tritosternum has a narrow base and pilose laciniae. The presternal shields are weakly sclerotized. The sternal shield (336–360 μm long) is finely reticulated (Fig. 10B). The setae are simple but *st.* I are the longest. The broadly oval anal shield is also reticulated. The paranal setae are short and simple, the postanal is minute and thornlike. The median opisthogastric setae are the longest, the laterals short like those on the dorsal membrane. The peritreme extends to the anterior margin of coxa I.

The tectum has a tapered broad central projection and is flanked by a pair of incurved horns (Fig. 10C). The chelicera is shown in figure 10D. The chaetotaxy of the palp trochanter, femur and genu is shown in figure 10E. The venter of the gnathosoma is shown in figure 10F: the corniculi are directed inwards slightly and the gnathosomal setae are strong, whilst the hypognathal denticles are well defined. The setae on leg I are mainly slender and simple but legs II–IV bear stouter setae. An erect barbed dorsal seta is present on genu III and similar but longer single setae are present on femur and tarsus IV.

MALE AND FEMALE. The adults have not been collected in the British Isles. Costa (1964) has reared this species in the laboratory and has figured all active developmental stages. Figures 10G–10K of the male and figures 10L–10P of the female are based on Costa's paper. The idiosoma of the male measures 1130–1295 μm long × 630–710 μm wide, and the female 1190–1480 μm long × 750–810 μm wide.

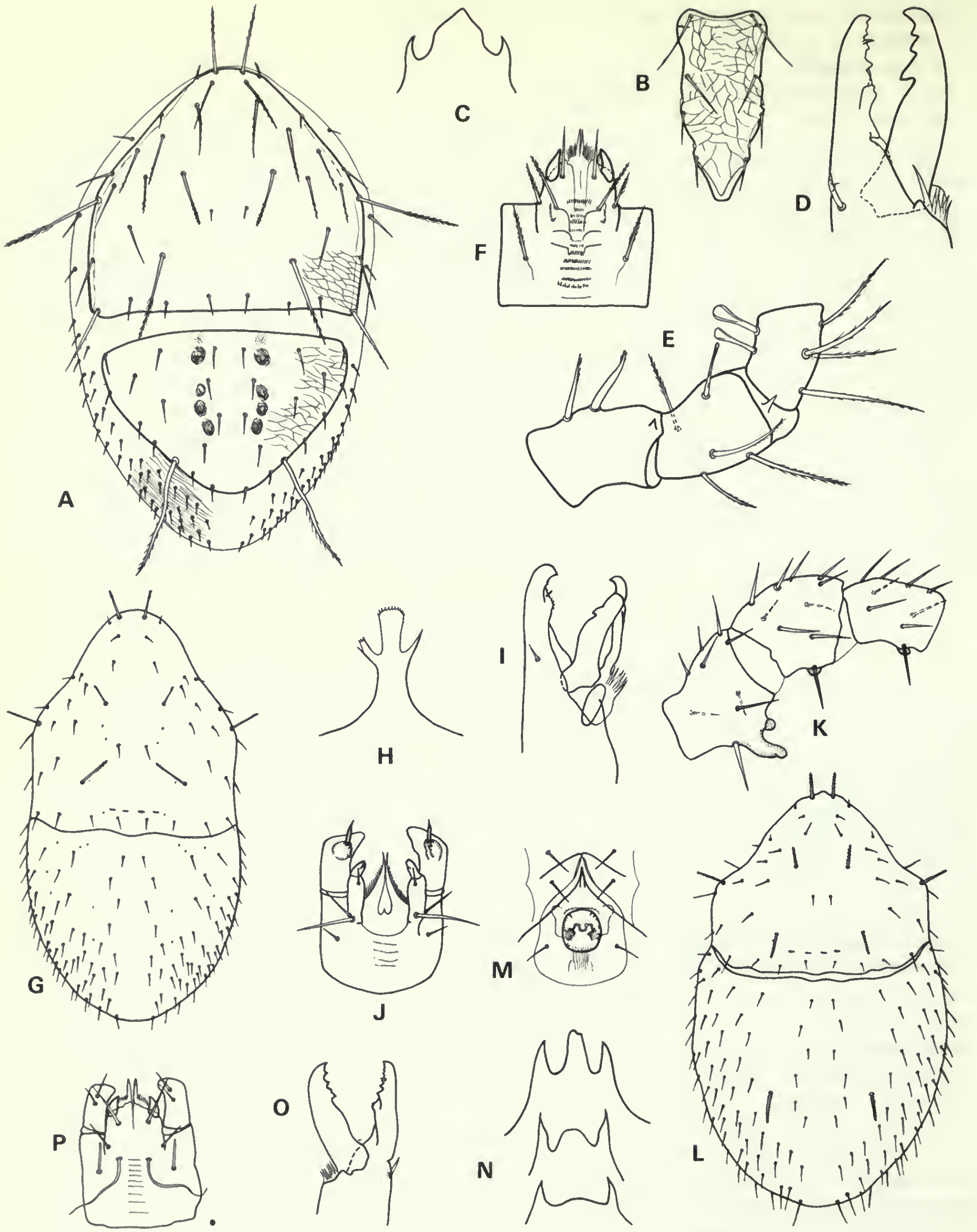


Fig. 10 *Parasitus copridis* Costa, **deutonymph** – A dorsum; B sternal shield; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma: **male** – G dorsum; H tectum; I chelicera; J venter of gnathosoma and palp trochanters; K femur, genu and tibia of leg II: **female** – L. dorsum, M genital region; N tectum showing variation; O chelicera; P venter of gnathosoma and palp trochanters. G–P after Costa, 1964.

MATERIAL EXAMINED. 12 samples – 111 DNN.
ENGLAND: Isles of Scilly, Surrey, Middlesex, Yorkshire, Northumberland.
SCOTLAND: Outer Hebrides (Shillay).

All were associated with beetles, eight samples were from *Geotrupes spiniger* (Marsham) and four were from *G. stercorarius* (L.).

DISTRIBUTION. Previously known only from *Copris hispanus* (L.) (Coleoptera) in Israel (Costa, 1963, 1964, 1966) and from unspecified beetles in Western Siberia (Davydova, 1976), this species is now recorded from the British Isles for the first time.

Parasitus evertsi Oudemans
(Fig. 11A–L)

Parasitus evertsi Oudemans, 1902*d*: 283, non synonym *Gamasus furcatus* G. & R. Canestrini, 1882: 49. Berlese, 1906: 172. Micherdzinski, 1969: 539. Type examined.

Oudemans (1902*d*) described *Parasitus evertsi* from a single female found in decaying leaves in the south of France. His slide is labelled 'Cauterets, Hautes Pyrenées, France, Aug. 1900, Jhr. Dr Ed. J. G. Everts'. I have compared the females examined during the present study with Oudemans's specimen and consider them to be conspecific. Berlese (1906) also examined Oudemans's type and synonymized *evertsi* with *Gamasus furcatus* G. & R. Canestrini, 1882, as he found few differences between the two species. Micherdzinski (1969) and Tichomirov (1969) cited this synonymy. Between 1906 and 1969 however, this does not appear to have been referred to. There have been several records of *furcatus* in recent years, viz. Schweizer (1961), Holzmann (1969), Micherdzinski (1969), Karg (1971) and Bregetova *et al.* (1977), and all refer to the true *furcatus* of G. & R. Canestrini in which the male chelicerae have the fixed digit enlarged distally. Additionally the male tectum is apparently characteristically bifid in *furcatus* and also the accessory spur on femur II is rounded and not angular as in *evertsi.* There is no doubt in my mind that the males and females of *evertsi* figured here are conspecific (five of the fifteen samples contained both sexes) and consequently this is the first description of the male of *evertsi.*

DEUTONYMPH. Unknown.

MALE. The idiosoma measures 890–936 μm long × 490–528 μm wide. It is entirely reticulated and heavily sclerotized and is divided by a transverse slit which generally results in the posterior and anterior portions of the dorsum overlapping. Many of the setae arise from raised bases. A pair of pores is located laterally a little anterior to the slit, and these are most conspicuous in specimens that are compressed (Fig. 11A). The podonotal region bears 21 pairs of setae of which *j1, j4, z5* and *r3* are long and stout and with fine pilosity. The remainder are short and with only traces of pilosity. The opisthonotal region bears about 21 pairs of setae which become stouter and more pilose posteriorly. In the specimen figured one seta of a pair (?*S5*) is deformed and bifid.

The tritosternum has a short narrow base, partly covered by the genital lamina, and pilose laciniae. The holoventral shield is strongly sclerotized and entirely reticulated (Fig. 11B). *St.* I are the longest of the sternal setae, *st.* II–IV becoming progressively shorter. The remaining ventral setae tend to become longer and stouter towards the posterior and show some degree of pilosity. The postanal seta is longer than the paranals. The peritreme extends to coxa I.

The tectum comprises a rounded central tine flanked by a pair of narrow tines that are either pointed or split distally (Fig. 11C). The chelicera is shown in figure 11D. The stout dorsal seta is inset. The chaetotaxy of the palp trochanter, femur and genu is similar to the female (Fig. 11L). The venter of the gnathosoma is as in figure 11E. The setae are fine and simple, the external posterior hypostomatic being the shortest. Leg I bears mainly simple slender setae. Leg II is shown in detail in figure 11F. Legs III and IV bear stouter setae generally than leg I and some are pilose, whilst ventrally several are thornlike.

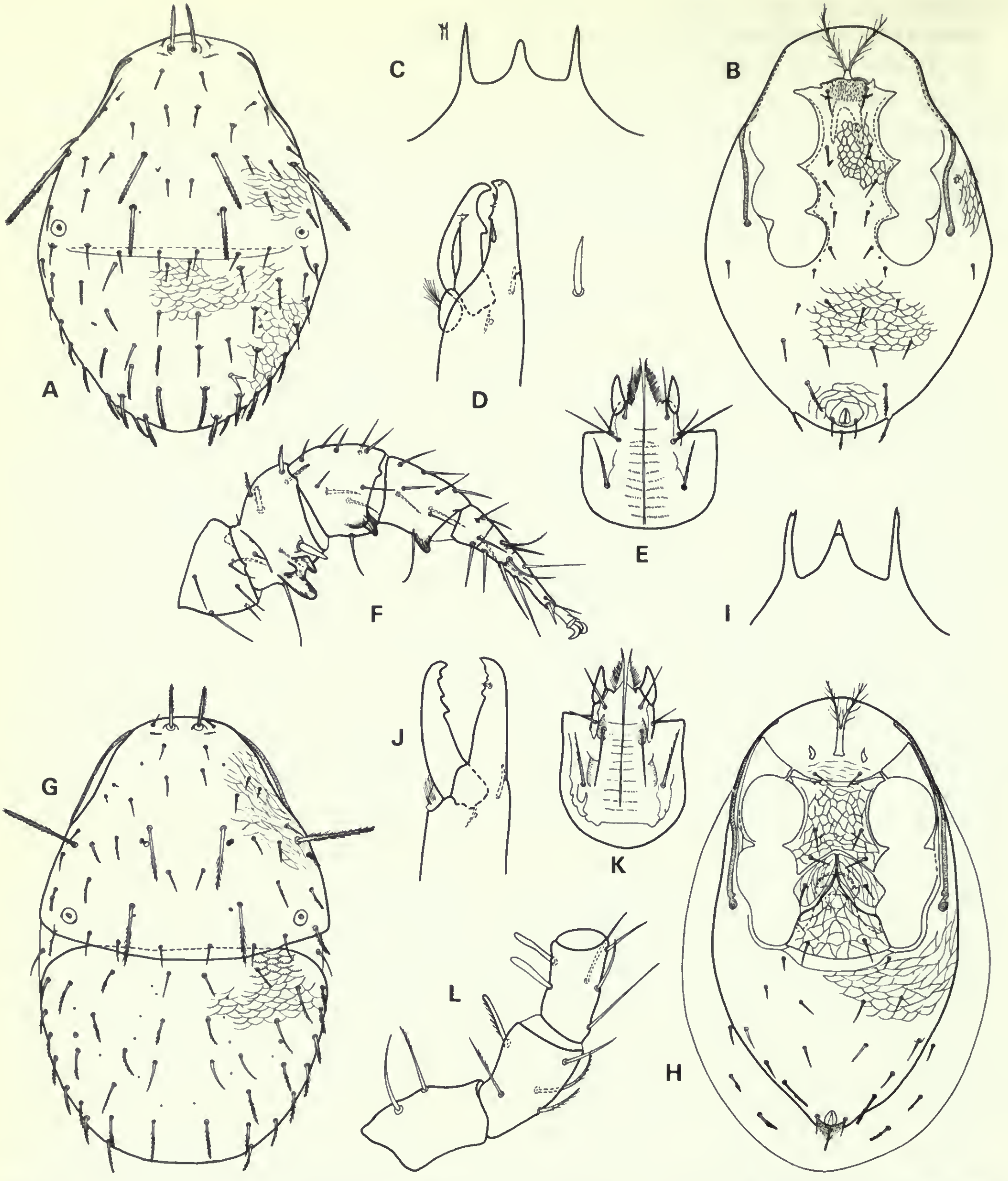


Fig. 11 *Parasitus evertsi* Oudemans, **male** – A dorsum; B venter; C tectum; D chelicera; E venter of gnathosoma; F leg II: **female** – G dorsum; H venter; I tectum; J chelicera; K venter of gnathosoma; L palp trochanter, femur and genu.

FEMALE. The podonotal shield (504–564 μm long × 600–636 μm wide) is well sclerotized and entirely reticulated and bears 21 pairs of setae and, like the male, it has a pair of conspicuous pores posterolaterally (Fig. 11G). As in the male also, setae *j1, j4, z5* and *r3* are long and stout with fine pilosity. The opisthonotal shield (432–480 μm long × 588–612 μm wide) is well sclerotized and entirely reticulated. It bears 17–20 pairs of setae which, like the male, become stouter and more pilose posteriorly.

The tritosternum has a narrow base and pilose laciniae. It is flanked by a pair of small crescentic presternal shields. The ventral shields are well sclerotized and entirely reticulated (Fig. 11H). Sternal setae I are situated on unsclerotized membrane anterior to the first pair of pores. All the sternogenital setae are simple. The genital shield is strongly pointed anteriorly. The opisthogastric shield bears seven pairs of setae of which the pair nearest the anus is pilose. The postanal seta is pilose at its tip and is longer than the simple paranals. The peritreme extends to coxa I.

The tectum (Fig. 11I) sometimes has the centre prong broken off and the lateral prongs are usually divided at their tips. The chelicera is shown in figure 11J, and the venter of the gnathosoma in figure 11K. The palpcoxal setae show slight pilosity. The chaetotaxy of the palp trochanter, femur and genu is shown in figure 11L. The setae of leg I are mainly fine and slender. Legs II and III bear some stout ventral setae and leg IV has a strong pilose dorsal seta (*c.* 125 μm) on the tarsus.

MATERIAL EXAMINED. 16 samples – 11♂♂, 18♀♀
ENGLAND: Cornwall, Devon, Dorset, Isle of Wight, Berkshire, Birmingham, Lancashire.
WALES: Monmouthshire, Caernarvonshire.
IRELAND: Leitrim.

Specimens were found in the following habitats: a cave, tree-holes, on *Sorex araneus* L., sewage filter beds, on bracket fungus, greenhouse soil, hedgerow debris, freshwater flood debris and seaweed.

DISTRIBUTION. This species has only been authentically recorded from the south of France (Oudemans, 1902*d*) (see discussion above).

Parasitus fimetorum (Berlese)
(Figs 12A–O; 13A–M; 14A–G)

Gamasus fimetorum Berlese, 1904*a*: 238; 1906: 135.
Eugamasus fimetorum: Holzmann, 1969: 14.
Parasitus fimetorum: Micherdzinksi, 1969: 478 (in part, see Karg, 1972: 57). Karg, 1971: 448.
Parasitus (Coleogamasus) fimetorum: Tichomirov, 1969: 1476. Bregetova *et al.*, 1977: 86, 89.
Parasitus affinis Oudemans, 1904*b*: 120. Berlese, 1906: 135.
Parasitus eta Oudemans & Voigts, 1904 in Voigts & Oudemans, 1904: 652. **Syn. nov.** Type examined.
Parasitus hibernicus Turk & Turk, 1952: 475. **Syn. nov.** Types examined.

This is the only species for which, during the course of the present study, larvae and protonymphs were both available, and the opportunity is taken to figure and describe briefly these two stages.

LARVA. The dorsum (*c.* 290 μm long × *c.* 180 μm wide) bears 18 pairs of simple setae distributed as in figure 12A: nine pairs are situated on the very weakly sclerotized and poorly defined podonotal shield and nine pairs on the unsclerotized opisthonotal cuticle. Setae *z5* are the stoutest and longest and are finely pilose.

The tritosternum has a long narrow base and the laciniae, which are strongly forked, are separated at their proximal ends by a bifid protrusion of the base (Fig. 12B). The sternal region bears three pairs of simple setae and is without trace of a sternal shield, whilst the anal shield, which is just discernible, bears the normal three setae associated with the anus and additionally a pair of euanal setae on the anal valves. However, as in *Pergamasus,* the paranal and postanal setae are exceptionally long in the larva, whilst the euanal setae will not be present in the protonymph. The remainder of the opisthogastric region bears four pairs of simple setae. Peritremes and stigmata are absent.

The tectum is trispinate with the broad centre prong weak and varying in length, the lateral prongs strong and slender (Fig. 12C, D). The chelicera is shown in figure 12E. The movable digit, which measures *c.* 33·6 μm, bears three conspicuous teeth, the teeth of the fixed digit are less well formed. The gnathosoma, which lacks hypognathal denticles and

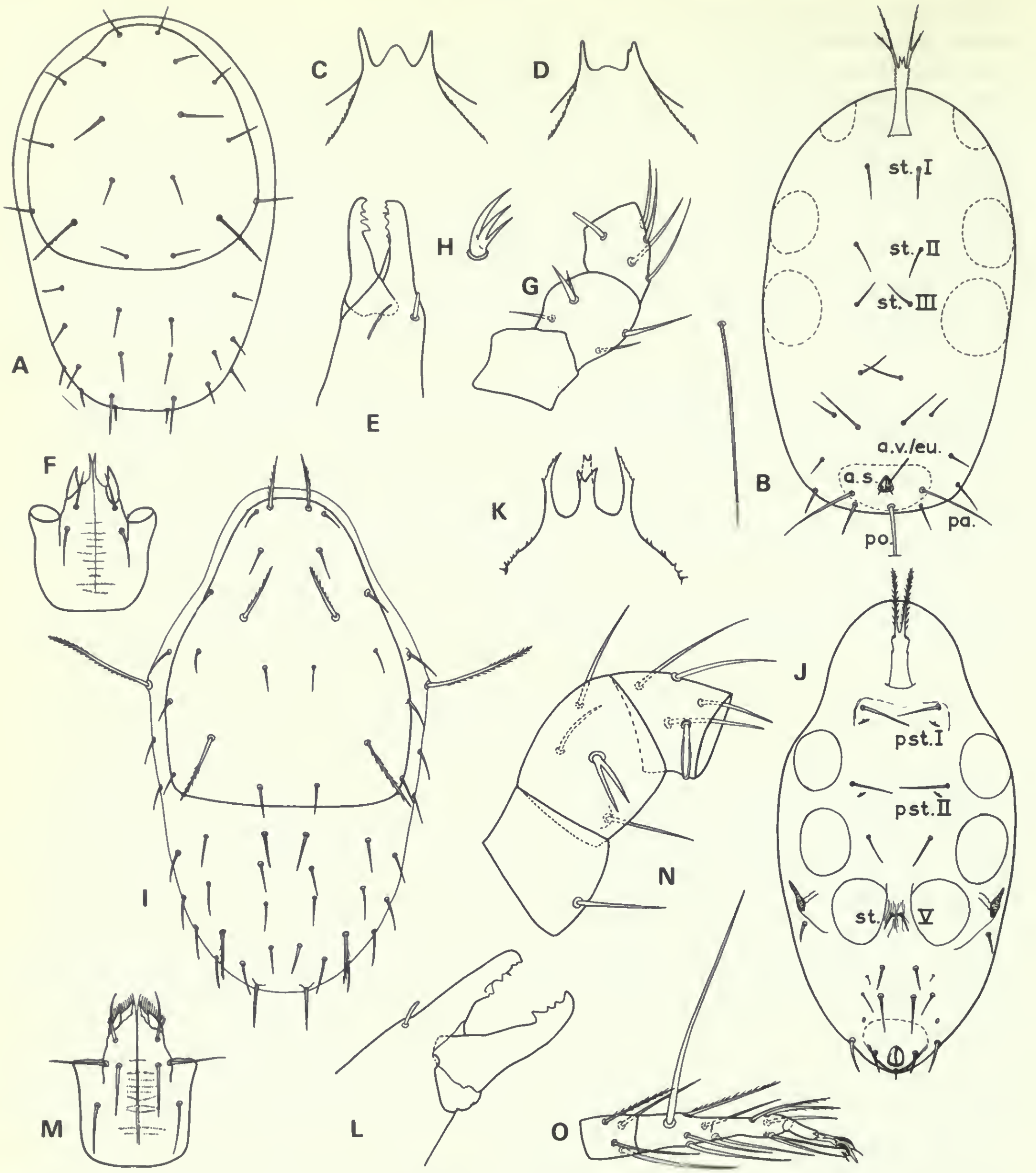


Fig. 12 *Parasitus fimetorum* (Berlese), **larva** – A dorsum; B venter; C, D tectum; E chelicera; F venter of gnathosoma; G palp trochanter, femur and genu; H apotele of palp tarsus: **protonymph** – I dorsum; J venter; K tectum; L chelicera; M venter of gnathosoma; N palp trochanter, femur and genu; O tarsus of leg IV. Abbreviations in text, p. 245.

bears only two pairs of ventral setae, the anterior hypostomatic and the external posterior hypostomatic, is shown in figure 12F. The palp trochanter is devoid of setae, whilst the femur and genu bear four and five setae respectively (Fig. 12G), and the strong tarsal apotele is three tined (Fig. 12H).

PROTONYMPH. In the protonymphal stage the podonotal shield is more clearly defined than in the larva and the opisthonotal region is generally stronger. The podonotal shield measures

288–324 μm long × 252–300 μm wide, whilst the opisthonotal region, still without clear sclerotization, measures 156–204 μm long × 216–264 μm wide (Fig. 12I). The podonotal region bears 15 pairs of setae of which 11 are situated on the shield, and the opisthonotal region bears 13 pairs.

The larval tritosternum is replaced at this stage by a form more typical of the deutonymphs and adults (Fig. 12J). The unsclerotized sternal region bears three pairs of simple setae and two pairs of pores, a fourth pair which are noticeably short, are situated on the membrane between coxae IV. The opisthogastric region bears six pairs of setae whose relative lengths are shown in the figure. The anal shield is smaller at this stage than in the larva and bears only the normal paranal and postanal setae – the larval euanals having disappeared. The stigma is situated opposite coxa IV and the peritreme extends anteriorly for approximately 38 μm.

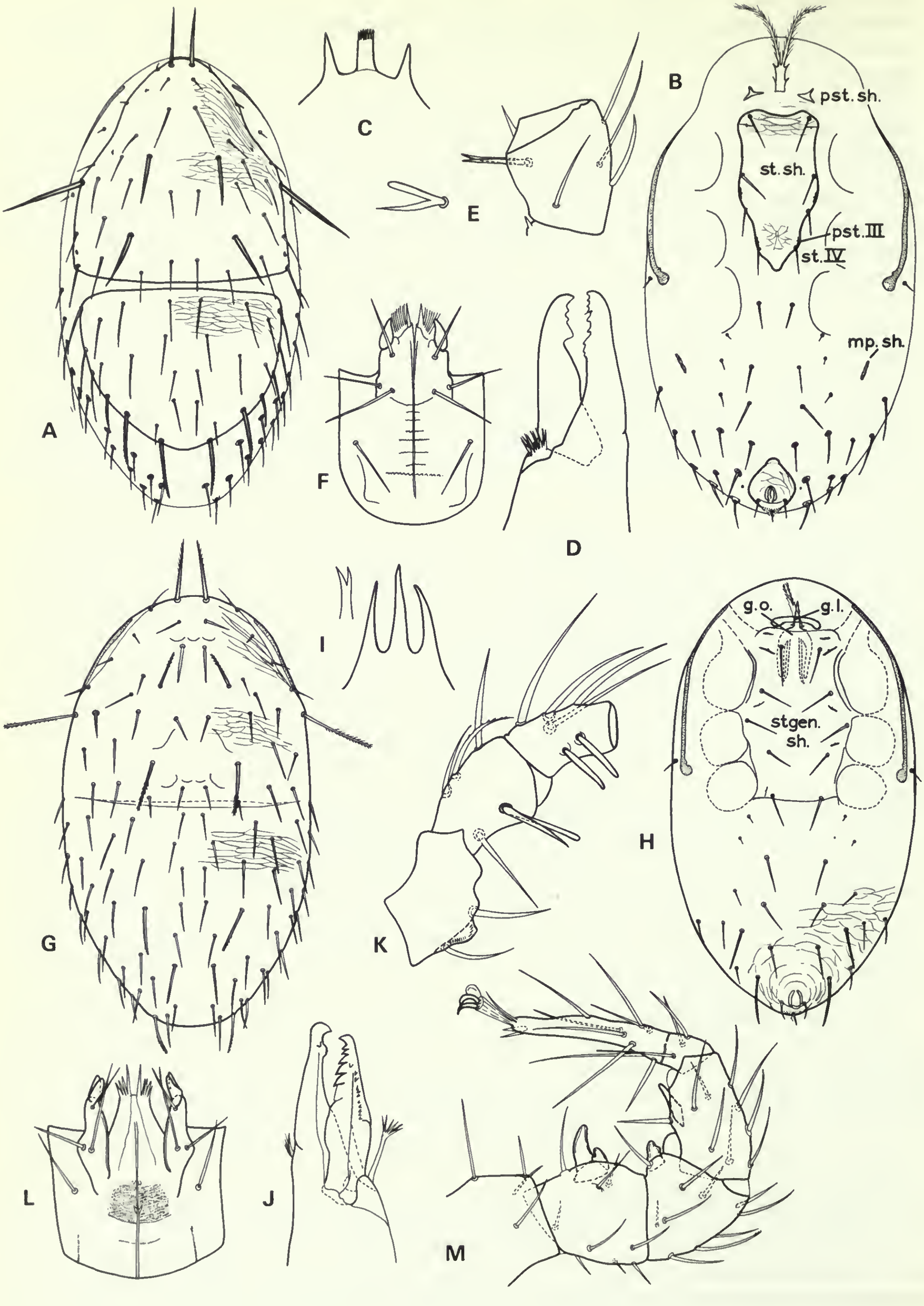
The tectum is trispinate and well developed (Fig. 12K), the only variation observed being in the bifurcation and breadth of the centre spine. The chelicera (Fig. 12L) is almost identical with that of the larva, whilst the venter of the gnasthosoma (Fig. 12M) has the full complement of setae and at least ten rows of hypognathal denticles. The chaetotaxy of the palp trochanter, femur and genu is shown in figure 12N. The leg setae are still basically simple although they are of less uniform length in that the proximal segments now bear a number of relatively shorter setae. Additionally, however, tarsus IV bears dorsally a long erect simple seta (*c.* 260 μm) (Fig. 12O) and the fine pilosity has disappeared from several others.

Deutonymph. The dorsal shields are strongly sclerotized, entirely reticulated and of noticeably constant outline (Fig. 13A). The podonotal shield (379–456 μm long × 354–500 μm wide) bears 20 pairs of setae, *s2* being situated off the shield. Setae *j1, j4, z5* and *r3* are considerably stouter and longer than the remainder which are, in this species, extremely fine and slender. The longest setae, *r3* (*c.* 170 μm), are also finely pilose. The opisthonotal shield (253–320 μm long × 328–470 μm wide) bears 15 pairs of setae of which two, *J5* and *Z3*, are stout and longer (90–95 μm) than the remainder (50–70 μm), and a third, *S4*, is also stout and measures *c.* 60 μm in length. The inner setae are very fine and slender. The setae on the posterior membrane are slightly stouter than the fine dorsal setae, and most arise from small platelets.

The tritosternum has a narrow base and strong pilose laciniae. It is flanked by clear but weakly sclerotized triangular presternal shields (Fig. 13B). The sternal shield (264–290 μm) bears four pairs of fine simple setae. Between *st.* I and close to the concave anterior edge of the shield lies a transverse area which appears, especially in uncleared specimens, to be unsclerotized. The egg-shaped anal shield bears the normal three setae associated with the anus, and the metapodal shields are slender and granular. The finely granular peritreme extends to the level of coxa I. The membrane posterior to the sternal shield bears approximately 16 pairs of simple setae, those nearest the anal shield arising from sclerotized platelets.

The tectum is trispinate with the centre prong almost invariably broken off (Fig. 13C) or even deformed. The chelicera is as in figure 13D. The palp femur is shown in figure 13E and the strongly forked anterolateral seta is also shown from a different angle. The two anterolateral setae on the palp genu are spatulate. The corniculi and gnathosomal setae are as in figure 13F. Only eight rows of hypognathal teeth are generally discernible. All setae on the legs are simple and of rather constant thickness. Tarsus IV bears dorsally a conspicuous erect seta *c.* 120 μm in length.

Male. The dorsum (880–960 μm long × 518–552 μm wide) is entire with a transverse suture (Fig. 13G). It is entirely reticulated but not usually heavily sclerotized. The dorsal chaetotaxy does not exhibit such extremes of setal length as for example *P. consanguineus* (Fig. 8I) although setae *j5, j6* and *J1–J4* are noticeably finer than the surrounding setae. The podonotal region bears 21 pairs of setae (although in the specimen figured *s3* on the left side is missing) of which *j1, j4, z5* and *r3* are conspicuously longer and stouter than the remainder.


A
B
pst. sh.
st. sh.
pst. III
st. IV
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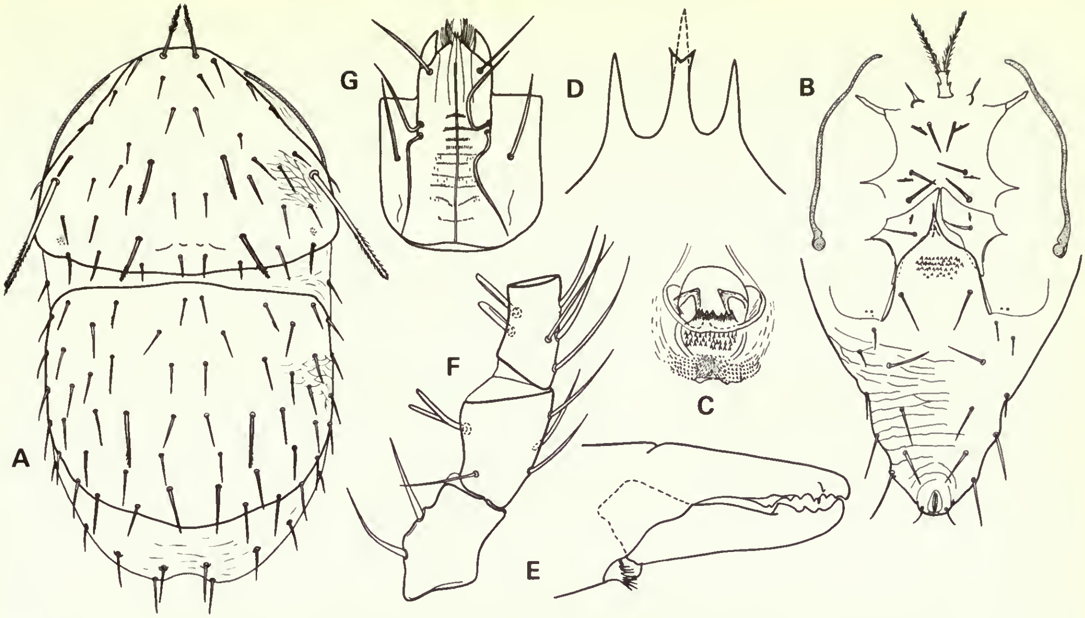

Fig. 14 *Parasitus fimetorum* (Berlese), **female** – A dorsum; B ventral sclerotization; C endogynium; D tectum; E chelicera; F palp trochanter, femur and genu; G venter of gnathosoma.

The opisthonotal region bears approximately 31 pairs of setae of which *Z3* are apparently the stoutest, although *Z2* and several in the *S*-series are almost as stout.

The tritosternum is small although appears in most specimens examined to show two short pilose laciniae and a rudimentary base. It is often completely covered by the protruding genital lamina (Fig. 13H). The sternogenital setae are simple. The paired paranal and single postanal setae are typically short, and the opisthogastric region bears approximately 11 pairs of setae of which the most posterior pair is the longest (*c.* 108 μm). The peritreme extends anteriorly to coxa I.

The tectum is trispinate with the outside prongs curved inwards, whilst the centre prong is either plain or forked at its tip (Fig. 13I). The chelicera is shown in figure 13J. The movable digit bears three large and two small teeth on the inner edge and a row of small pointed teeth lower on the inner face, the spermatodactyl lies close to the digit. The fixed digit bears only a cusp of small denticles distally. The palp trochanter, femur and genu are shown in figure 13K: the trochanter bears a shallow keel-like ridge ventrally. The corniculi are strongly stalked and deeply cleft (Fig. 13L), and the gnathosomal setae are simple whilst the normal row of hypognathal denticles is replaced by an area of rasp-like projections. The leg setae are similar to those of *P. consanguineus,* the slightly stouter ones being generally finely pilose on at least one margin. Leg II is shown in detail in figure 13M. No significant variation has been observed in the form of the spurs.

FEMALE. The podonotal shield (456–540 μm long × 432–528 μm wide) bears 21 pairs of setae of which *j1, j4, z5* and *r3* are conspicuously longer and stouter than the remainder and are usually finely pilose (Fig. 14A). The opisthonotal shield (425–504 μm long × 444–570 μm wide) bears 26 pairs of setae of which *Z3* are usually the stoutest and are finely pilose. The posterior interscutal membrane bears only about five pairs of setae dorsally. Both shields are

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Fig. 13 *Parasitus fimetorum* (Berlese), **deutonymph** – A dorsum; B venter; C tectum; D chelicera; E palp femur and anterolateral seta; F venter of gnathosoma: **male** – G dorsum; H venter; I tectum; J chelicera; K palp trochanter, femur and genu; L venter of gnathosoma; M leg II. Abbreviations in text, p. 245.

very weakly sclerotized and in fact few specimens have been examined in which the shields can be delineated clearly. Additionally, although the figure illustrates a typical example, variations in setal thickness and length are common without being extreme enough to warrant additional illustration. The idiosoma is characteristically concave postero-medially giving a 'waisted' appearance.

The tritosternum has a narrow base and pilose laciniae. It is flanked by a pair of weakly sclerotized presternal shields of a constant and conspicuous form (Fig. 14B). The sternal shield is very weakly sclerotized and bears three pairs of strong simple setae. The metasternal and genital setae are less stout. The genital shield is strongly pointed anteriorly, but posteriorly it merges into the weakly sclerotized and narrow opisthogastric shield. The most conspicuous elements of the endogynium are shown in figure 14C, but there is often considerable distortion and displacement of the individual structures. The three anal setae are short as are three of the eight pairs of opisthogastric setae. The peritreme extends anteriorly to coxa I.

The tectum is trispinate with the median prong either long and pointed or shorter and regularly bifid (Fig. 14D). The chelicera is shown in figure 14E, the chaetotaxy of the palp trochanter, femur and genu is as in the male, but the trochanter lacks the ventral keel-like ridge (Fig. 14F). The corniculi are broad and smooth. The gnathosomal setae are simple with the posterior hypostomatics long and contorted (Fig. 14G). There are usually ten pairs of conspicuous hypognathal denticles. The leg setae are simple although many are sinuous to some degree.

MATERIAL EXAMINED. 128 samples – LL, PNN, 399 DNN, 65 ♂♂, 105 ♀♀, plus some half a dozen samples containing almost countless specimens of all stages from larva to adult.

ENGLAND: Cornwall, Isles of Scilly, Devon, Dorset, Somerset, Gloucestershire, Bristol, Berkshire, Isle of Wight, Hampshire, Sussex, Middlesex, London, Kent, Surrey, Essex, Hertfordshire, Buckinghamshire, Norfolk, Suffolk, Cambridgeshire, Northamptonshire, Birmingham, Staffordshire, Lancashire, Cheshire, Cumberland, Yorkshire, Northumberland.

WALES: Anglesey, and North Wales (no precise locality, see below).

SCOTLAND: Berwickshire, Dunbartonshire, Aberdeenshire, Inner Hebrides (Muck, Iona, Ulva).

IRELAND: Cork, Wexford, Kildare, Meath, Westmeath.

CHANNEL ISLANDS: Jersey.

This is one of the most widespread European species of *Parasitus* and is distributed throughout the British Isles. The bulk of the material examined is from stacked rotting vegetation, compost, manure and dung. Some is from small mammal nests (*Sorex, Neomys, Talpa, Microtus, Apodemus, Micromys*), some associated with beetles (*Aphodius, Geotrupes, Nicrophorus, Atholus*) and bumblebees (*Bombus*) and also occasionally from birds' nests (*Rissa, Vanellus, Delichon, Riparia*), and some from poultry litter (Brady, 1970), bat dung, and from a dead fox *Vulpes vulpes* (L.) (Smith, 1975). Few records only are from leaf litter, mosses or grassland. The only specimens examined from the seashore are two deutonymphs from seaweed, Benllech, Anglesey, October 1961, coll. P. N. Lawrence. Halbert (1920) does not mention this species in 'The Acarina of the Seashore' and I have not found it in similar samples collected by myself on the Isles of Scilly or in north Kent.

DISTRIBUTION. Previous British records are from the Tyne Province and also Lancashire, Yorkshire and Cheshire (Hull, 1918), Ireland (Halbert, 1915), Hertfordshire (Hyatt, 1956), the Channel Islands (Browning, 1956), Huntingdonshire (Davis, 1970) and London (Smith, 1975). Hill & Gordon (1945) recorded '*Parasitus* sp. 10 nymphs' from the straw used to stuff the palliasses of American servicemen stationed in North Wales (the localities could not be given at the time). I have examined one of these specimens and it is a deutonymph of *fimetorum*.

It is recorded from Iceland (Sellnick, 1940), Holland (Oudemans Collection), Belgium (van

Daele & Heungens, 1974, 1975), Germany (several authors, see Micherdzinski, 1969), Austria (Irk, 1941, Leitner, 1946), Switzerland (Schweizer, 1949, 1961), Italy (Berlese, 1906), Poland (Micherdzinski, 1969). U.S.S.R. (Pinchuk, 1976), Western Siberia (Davydova, 1969, 1976), and Canada (Richards, 1976, Richards & Richards, 1976). Like the British material examined, most records are from composts and dung. The inclusion of Israel (Bodenheimer, 1949) by Micherdzinski (1969 : 484) is in error. Bodenheimer specifically stated (p. 33) that his ectoparasites had not been identified beyond orders. The record of Costa (1961) from Israel is referrable to *Parasitus bituberosus* Karg, 1972, as are presumably Costa, 1962, 1963 and 1966.

Parasitus hyalinus (Willmann)
(Fig. 15A–L)

Eugamasus hyalinus Willmann, 1949*a*: 110. Holzmann, 1969: 15.
Parasitus hyalinus: Micherdzinski, 1969: 529. Karg, 1971: 447.
Parasitus (Vulgarogamasus) hyalinus: Bregetova *et al.*, 1977: 80.

DEUTONYMPH. This description is taken from three very weakly sclerotized specimens, two of which are moulting to females. The podonotal shield averages 250 μm long × 265 μm wide. It is lightly reticulated and bears 20 pairs of simple setae (Fig. 15A). Setae *s2* are off the shield, *r3* are the longest and *z5* are barely longer than adjacent setae. The opisthonotal shield averages 180 μm long × 250 μm wide, bears 14–15 pairs of simple setae, and is lightly reticulated. The setae on the posterior membrane are short.

The tritosternum has a narrow base and pilose laciniae. The sternal shield measures *c.* 180 μm long and is in outline more characteristic of some *Pergamasus* species (Fig. 15B). It is lightly reticulated and the setae are simple. The presternal shields are rudimentary. The opisthogastric setae are simple and the anal shield is oval in outline with the anal setae simple. The extremely narrow peritreme extends to coxa I.

The tectum of two of the specimens is as in figure 15C and of the third specimen in figure 15D. The chelicerae appear to be as in the female (Fig. 15J). The chaetotaxy of the palp trochanter, femur and genu is as in figure 15E, and the venter of the gnathosoma is as in figure 15F. The setae of leg I are extremely fine and slender. Those on leg II are a little stouter, especially on the tarsus, and on legs III and IV they are progressively stouter, with those on tarsus IV the heaviest. Tarsus IV bears dorsally a single erect seta *c.* 110 μm long.

MALE. Unknown.

FEMALE. The podonotal shield (290–350 μm long × 230–350 μm wide when flattened) is reticulated mainly around the lateral margins. It bears 22 pairs of simple setae in at least three of the specimens examined, as these have *r4* situated on the shield. The area posterior to *r3* is generally folded ventrally, but Holzmann (1969) figures *r4* off the shield. In the specimen figured an additional very slender seta is present on the right side between *s5* and *s6* (Fig. 15G). Setae *r3* are the longest (*c.* 70 μm). The opisthonotal shield (250–270 μm long × 300–380 μm wide when flattened) is of similar structure to the podonotal shield and bears 26 pairs of simple setae.

The tritosternum has a narrow base and pilose laciniae and, as in the deutonymph, the presternal shields are extremely small (Fig. 15H). The ventral shields are very weakly sclerotized. The sternal setae are simple, *st.* II and III being stouter than *st.* I. The metasternal, genital and anal setae, together with all eight pairs of opisthogastric setae, are fine and slender. The genital shield is pointed anteriorly. Two conspicuous granular areas may be present in the endogynium.

The trispinate tectum is shown in figure 15I, and the chelicera in figure 15J. The movable digit is 55 μm long. The gnathosomal setae are rather stout and the posterior hypostomatics tend to be somewhat sinuous (Fig. 15K). The chaetotaxy of the palp femur and genu is as in figure 15L. The leg setae are similar to the deutonymph, but tend to be generally stouter. The long dorsal seta on tarsus IV is *c.* 95 μm.

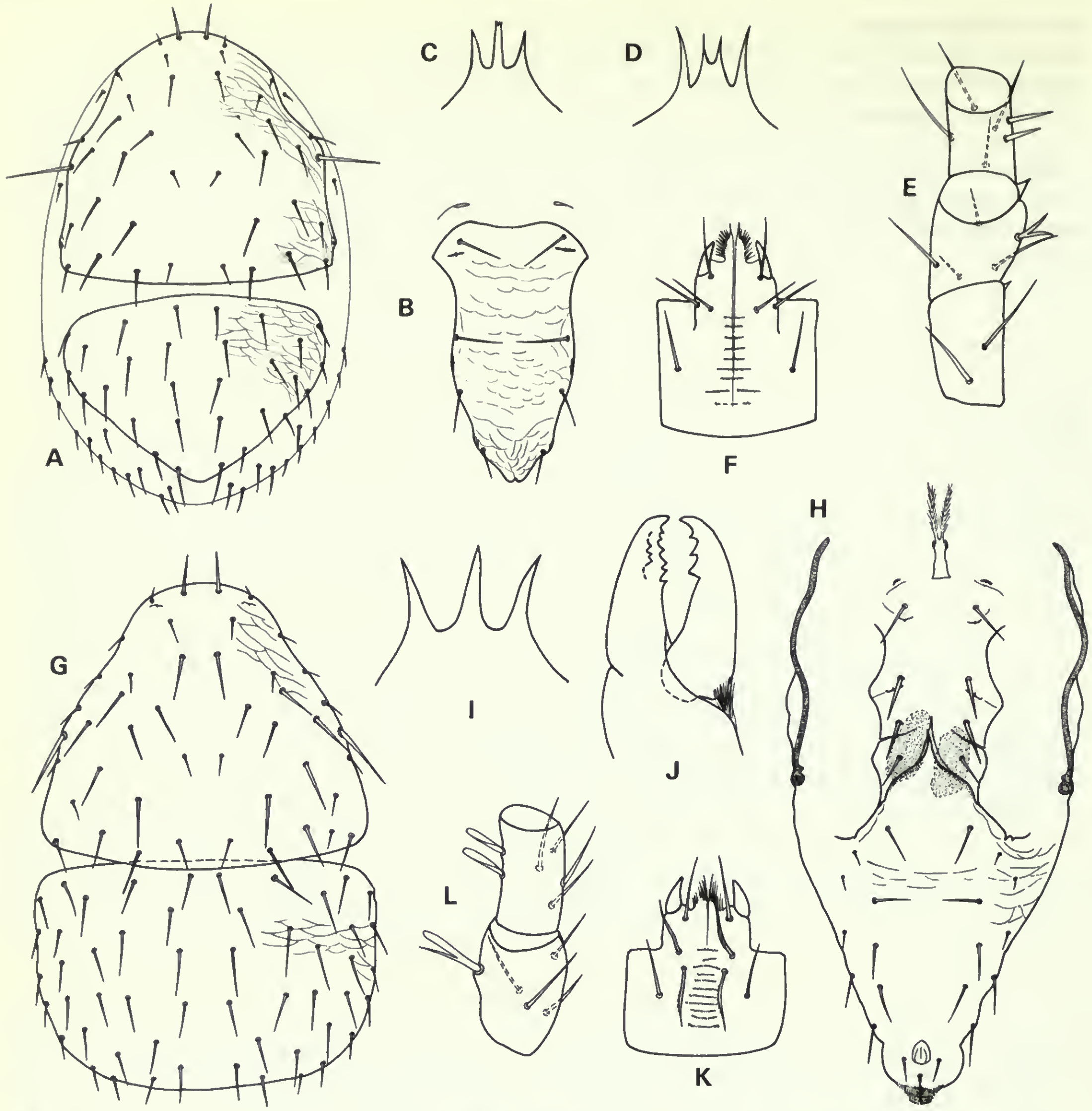


Fig. 15 *Parasitus hyalinus* (Willmann), **deutonymph** – A dorsum; B sternal shield; C, D tectum; E palp trochanter, femur and genu; F venter of gnathosoma: **female** – G dorsal shields; H ventral sclerotization; I tectum; J chelicera; K venter of gnathosoma; L palp femur and genu.

MATERIAL EXAMINED. 5 samples – 3 DNN, 17 ♀♀.

ENGLAND: One female from the nest of a sand martin *Riparia riparia,* Send, Surrey, 4 June 1971, two females from manure in a mushroom farm, Tuckton, Hampshire, 7 December 1949, thirteen females from mushroom compost, Nuneaton, Warwickshire, October 1959, one female from grassland, Sutton Bonington, Leicestershire, 21 August 1977, and three deutonymphs from manure heaps, Ivinghoe, Buckinghamshire, 3 March 1962.

IRELAND: In grassland, Johnstown Castle, Co. Wexford (Prof. G. O. Evans, *in litt.*).

DISTRIBUTION. This species is recorded for the first time from the British Isles. It has been found in Poland (Willmann, 1949*a,* Micherdzinski, 1969) and Germany (Karg, 1965, Holzmann, 1969), in most cases associated with compost.

Parasitus insignis (Holzmann)
(Fig. 16A–P)

Eugamasus insignis Holzmann, 1969: 20.
Parasitus insignis: Micherdzinski, 1969: 533. Karg, 1971: 448.
?Pergamasus (Paragamasus) diviortus Athias-Henriot, 1967: 23
Parasitus (Neogamasus) diviortus: Tichomirov, 1971: 804. Bregetova *et al.,* 1977: 75, 77.

Tichomirov (1971) synonymizes *Eugamasus insignis* Holzmann, 1969 and *Parasitus (Neogamasus) rasumovskyi* Tichomirov, 1969 with *Pergamasus (Paragamasus) diviortus* Athias-Henriot, 1967. Athias-Henriot (1967), in her observations on *Pergamasus* subgenus *Paragamasus* Hull, 1918, includes *Parasitus islandicus* Sellnick, 1940. Karg (1971) also recognizes that *islandicus* and the related species *Parasitus insignis* Holzmann, 1969 show affinities to both *Pergamasus* and *Parasitus*, but he concludes that they should be placed in *Parasitus.* Tichomirov (1969) designates *islandicus* as the type of his new subgenus *Neogamasus* to which he adds five other species, one of which is *rasumovskyi.*

The species identified here as *Parasitus insignis* (Holzmann) is based on a single female which matches perfectly Holzmann's figures and measurements. For the present I feel that until more material, including males and deutonymphs, can be examined, there is little to be gained in speculating further on the taxonomic position of this specimen.

DEUTONYMPH. So far this stage has not been found in the British Isles. Figures 16A–D are from Holzmann (1969) who did not give individual measurements for the podonotal and opisthonotal shields, merely giving the size as 580 × 410 μm.

MALE. This stage also has not been recorded from the British Isles. Figures 16E–I are from Holzmann (1969) who gives the measurements of the idiosoma as 730 × 480 μm. Karg (1971) illustrates trochanter IV, which bears a small dorsal protuberance as in the female (Fig. 16P).

FEMALE. The podonotal shield in the specimen examined measures 430 μm long × 430 μm wide. It is finely granular, lightly but entirely reticulated, and bears 22 pairs of slender simple setae (Fig. 16J), the longest being *r3* (140 μm or longer). Setae *r4* are situated on the shield. The opisthonotal shield measures 380 μm long × 430 μm wide. The reticulations are more prominent than on the podonotal shield, and in the anterior half at least, are conspicuously transverse. There are 27 slender simple setae on the left side and 25 on the right.

The tritosternum has a narrow base and pilose laciniae. It is flanked by a pair of symmetrical and fragmented presternal shields (Fig. 16K). The ventral shields are reticulated, and with the exception of the area anterior to sternal setae I, are densely granular. The opisthogastric area bears ten setae on the left side and nine on the right. All ventral setae are slender and simple. The anal setae are short. The peritreme does not reach coxa I.

The tectum is trispinate with the centre prong only slightly longer than the laterals (Fig. 16L). The chelicera is shown in figure 16M. The teeth on the fixed digit figured do not coincide in position with those on the second chelicera. The chaetotaxy of the palp trochanter, femur and genu is as in figure 16N, and the venter of the gnathosoma in figure 16O. The hypognathal denticles are exceptionally clear and symmetrical. Leg I bears slender setae, a few of which are finely pilose. Leg II bears generally stouter setae, especially on the tarsus, and ventrally on the other segments. Leg III is similar to leg II. Trochanter IV bears a small dorsal protuberance (Fig. 16P), but the remaining segments of both legs IV are missing.

MATERIAL EXAMINED. 1 ♀

ENGLAND: A single female from clay loam with rye-grass, Jeallott's Hill, Berkshire, 13 November 1969, coll. W. Wilkinson.

DISTRIBUTION. Previously known only from house-plant soil, Erlangen, Germany, where Holzmann (1969) collected many deutonymphs, males and females, this species is recorded from the British Isles for the first time.

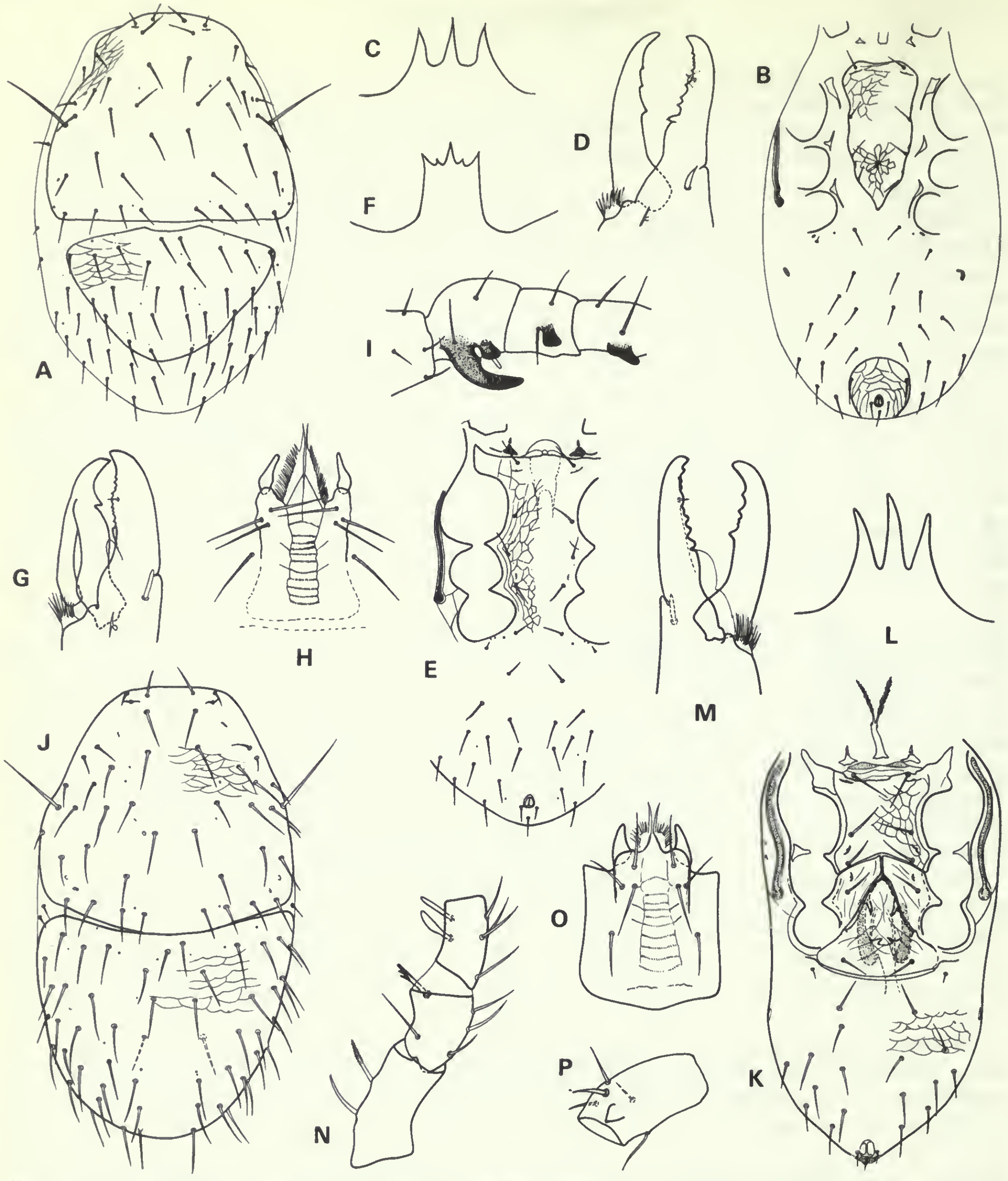


Fig. 16 *Parasitus insignis* (Holzmann), **deutonymph** – A dorsum; B venter; C tectum; D chelicera: **male** – E venter; F tectum; G chelicera; H venter of gnathosoma; I armature of leg II: **female** – J dorsum; K venter; L tectum; M chelicera; N palp trochanter, femur and genu; O venter of gnathosoma; P trochanter of left leg IV from above. A–I after Holzmann, 1969.

Parasitus kempersi Oudemans

(Figs 17A–M; 18A–F)

Parasitus kempersi Oudemans, 1902*b*: 36. Micherdzinski, 1969: 486. Karg, 1971: 448.
Parasitus (Coleogamasus) kempersi: Tichomirov, 1969: 1476. Bregetova *et al.*, 1977: 86, 89.
Gamasus (Gamasus) kempersi: Berlese, 1906: 143.
Eugamasus kempersi: Holzmann, 1969: 14.

DEUTONYMPH. The podonotal shield (430–444 μm long × 408–480 μm wide) is reticulated and bears 20 pairs of setae, *s2* being situated off the shield. Setae *j1, j4, z5* and *r3* are long, stout and pointed with very fine pilosity at their tips whilst the remainder are short and fine (Fig. 17A). The opisthonotal shield averages 305 μm long × 430 μm wide and is also reticulated. It has a conspicuous median mark posteriorly often accompanied by a slight invagination. Fifteen pairs of setae are present of which *Z3* are long and stout and *J5* are thornlike, as are to a certain extent three pairs on the membrane immediately posterior.

The tritosternum is flanked by a pair of slender angular presternal shields. The sternal shield (Fig. 17B) is reticulated and the setae are simple. The anal shield is oval and reticulated with the setae simple, the postanal being the shortest. The opisthogastric setae are generally longer than the setae on the dorsal membrane. The metapodal shields are slender and granular and the peritreme extends to coxa I.

The tectum is trispinate and occasionally the centre prong is irregularly forked (Fig. 17C). The fixed digit of the chelicera bears four or more small teeth and two larger, whilst the movable bears two small teeth and one larger (Fig. 17D). The palp trochanter, femur and genu are shown in figure 17E. The venter of the gnathosoma is as in figure 17F: all setae are simple. The leg setae are almost entirely strong and simple, but tarsus IV bears a stout erect finely pilose seta dorsally.

MALE. The dorsum (1044–1100 μm long × 528–540 μm wide) is completely covered by a lightly reticulated shield which is divided medially by a full-width transverse suture, the two parts often overlapping (Fig. 17G). The podonotal region bears about 22 pairs of setae of which four pairs, *j1, j4, z5* and *r3*, are long, stout and finely pilose, and three pairs, *z1, r2* and *s5* are conspicuously more thornlike than the remaining fine setae. The opisthonotal region bears over 26 pairs of setae of which *Z3* are the stoutest and longest, and *J1, J2, S2* and several posterior to *Z3* are thornlike, but the remainder are fine and short.

The tritosternum is apparently absent – a fact noted by Halbert (1915) – and the genital lamina extends well forward of the anterior margin of the sternogenital shield. Slender oblique presternal shields are present (Fig. 17H). The venter is lightly reticulated and all setae are slender and fine except for one pair immediately anterolateral to the anus, and also the postanal which is the stoutest and longest. These three setae are finely pilose. The peritreme extends to coxa I.

The tectum is indistinct (Fig. 17I), but nevertheless it scarcely resembles that of the deutonymph or even the female. The chelicera is shown in figure 17J. The movable digit is provided with a row of up to a dozen sharp backwardly-projecting teeth and a second shorter row of similar teeth, whilst the fixed digit has a finely serrated inner margin. The chaetotaxy of the palp trochanter, femur and genu is as in figure 17K. One of the two setae on the trochanter is modified and is stout and bifid. The stalked corniculi are pointed and the internal posterior hypostomatics are considerably longer than the other three pairs of gnathosomal setae (Fig. 17L). The hypognathal denticles are usually indistinct. Leg II is shown in detail in figure 17M. The setae of the remaining legs show no strong characteristics – they are generally strong and the stouter ones are often pilose.

FEMALE. The dorsal shields are completely reticulated and their chaetotaxy is the same as in the male (Fig. 17G), except that the membrane posterior to the opisthonotal shield bears setae that in the male are naturally on the shield. The podonotal shield measures 504–540 μm long × 600–684 μm wide and the opisthonotal shield 540–600 μm long × 588–636 μm wide.

The tritosternum has a short narrow base and pilose laciniae. Presternal shields are absent. The sternal region is very weakly sclerotized although faint reticulations are present especially in the opisthogastric region (Fig. 18A). The genital shield is pointed medially and the more conspicuous parts of the endogynium are shown. The opisthogastric region bears eight pairs of setae of which six are relatively long and stout. The two marginal pairs nearest the anus are the strongest and, like the postanal seta, and one pair on the adjacent membrane, are finely pilose. The paranals are short and fine. The peritreme extends to coxa I.

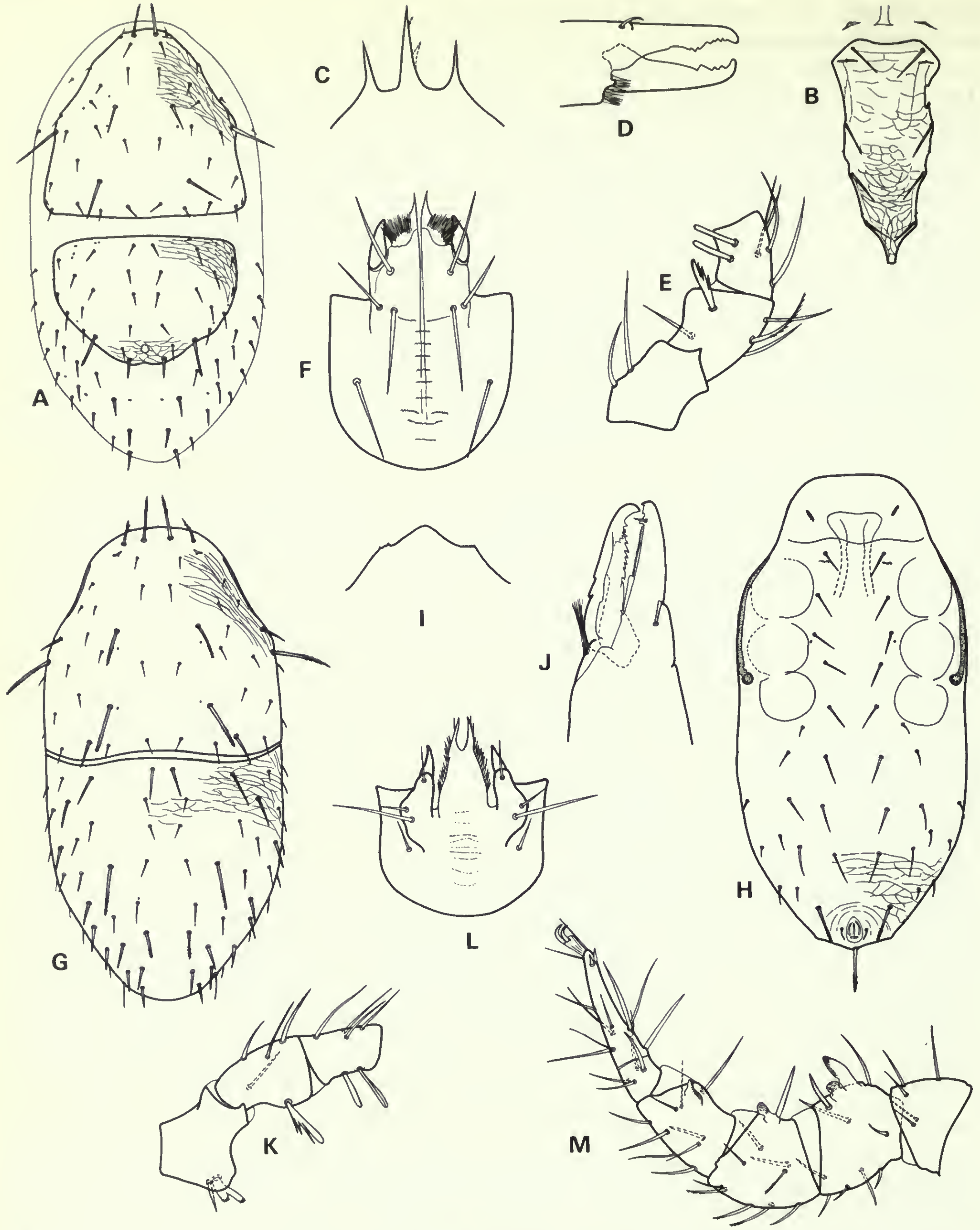


Fig. 17 *Parasitus kempersi* Oudemans, **deutonymph** – A dorsum; B sternal shield; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma: **male** – G dorsum; H venter; I tectum; J chelicera; K palp trochanter, femur and genu; L venter of gnathosoma; M leg II.

The tectum is trispinate and shows a certain amount of variation (Figs 18B, C). The chelicera is as in figure 18D. The chaetotaxy of the palp trochanter, femur and genu is shown in figure 18E, and the venter of the gnathosoma in figure 18F. The stout posterior

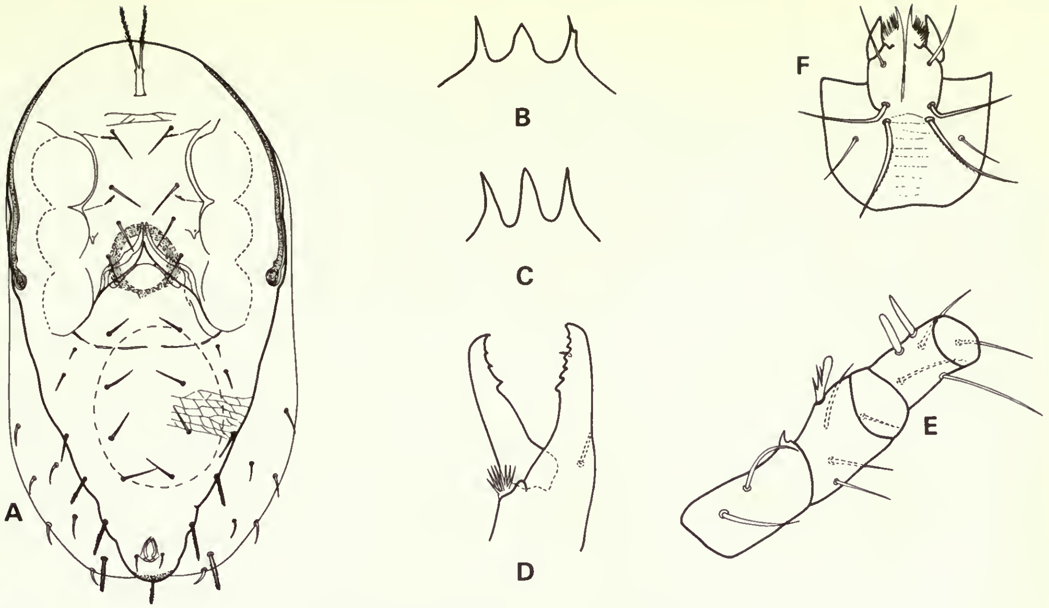


Fig. 18 *Parasitus kempersi* Oudemans, **female** – A venter; B, C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma.

hypostomatic setae are the longest and are often bent, but not to the same extent as in *P. fimetorum* (Fig. 14 G). The leg setae are in general shorter than in most species and some dorsal setae on the proximal segments of legs III and IV tend to be peglike.

This species is weakly sclerotized and bursts easily on clearing in lactic acid.

Material examined. 38 samples – 104 DNN, 88 ♂♂, 94 ♀♀, plus some dozen samples with almost countless deutonymphs, males and females, of which a selection were examined closely.

England: Cornwall, Isles of Scilly, south Devon, Dorset, north Kent, Lancashire (Walney Island), Northumberland, Durham.

Wales: Caernarvonshire (Llandudno and Bangor), Anglesey.

Scotland: Argyllshire (Loch Sween), Inverness-shire (Moray Firth coast), Outer Hebrides (Harris).

Ireland: Cork, Clare.

This often abundant and exclusively seashore species is probably found throughout the British Isles where tidal debris occurs.

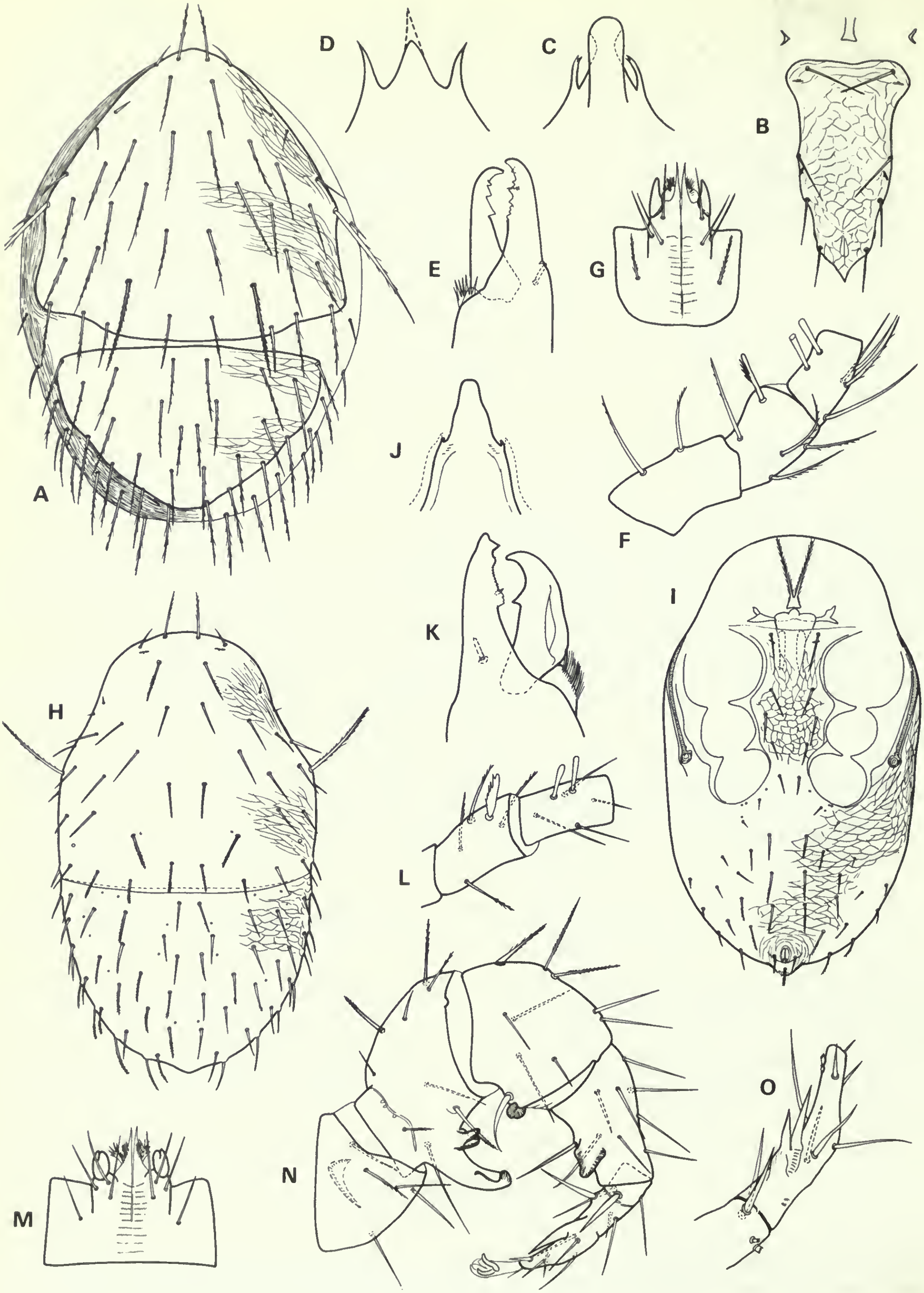
Distribution. Previous British records are from Co. Mayo and Co. Dublin (Halbert, 1915, 1920), Northumberland (Hull, 1918), Devon and Dorset (Evans & Browning, 1954) and Co. Durham (Egglishaw, 1965). The record of *Parasitus kempersi,* identified by Vitzthum, from Bagley Wood near Oxford (Elton *et al.,* 1931), is clearly a misidentification.

It is recorded from Iceland (Sellnick, 1940), Norway (Berlese, 1906), Holland (Oudemans, 1902*b*), Germany (Willmann, 1939*b*, Neumann, 1941, Holzmann, 1969) and Italy (Berlese, 1906).

Parasitus loricatus (Wankel)

(Figs 19 A–O; 20 A–G)

Gamasus loricatus Wankel, 1861: 261 (♀).
Eugamasus loricatus: Oudemans, 1914, Heft 8: 114. Holzmann, 1969: 17. Davydova, 1969: 17, 19.
Parasitus (Eugamasus) loricatus: Tichomirov, 1969: 1475. Davydova, 1976: 41. Bregetova *et al.,* 1977: 65, 69.


D
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Gamasus niveus: Wankel, 1861: 262 (♂).
Eugamasus niveus: Trägårdh, 1912: 536.
Parasitus niveus: Micherdzinski, 1969: 552. Karg, 1971: 448.
Paracarpais (Gigacarpais) niveus: Athias-Henriot, 1978: 48.
Gamasus crassus Kramer, 1876: 86.
Gamasus anglicus Hull, 1918: 83. Micherdzinski, 1969: 553.
Eugamasus anglicus: Turk, 1953: 10.
Parasitellus ferox (Trägårdh, 1910) sensu Turk & Turk, 1952: 478 = *Parasitus loricatus* (Wankel, 1861) and *Porrhostaspis lunulata* Müller, 1859, non Trägårdh, 1910 = *Parasitellus fucorum* (De Geer, 1778).

DEUTONYMPH. Normally the future adult sex of parasitine deutonymphs can only be determined when the development of the male or female is far enough advanced to be discernible beneath the cuticle of the deutonymph following clearing in lactic acid. At this stage such specific features as the adult chelicerae and tectum, or the gnathosomal setae in the females of *P. fimetorum,* the sternal setae in the females of *P. consanguineus,* and the spur on the palp trochanter of the male of *Vulgarogamasus oudemansi,* are not difficult to see. However, in *P. loricatus* the deutonymphs themselves show sexual dimorphism in the form of the tectum as described below.

The dorsal shields are not heavily sclerotized although they are strongly reticulated and the setae are remarkably homogeneous (Fig. 19A). The podonotal shield (432–516 μm long × 468–576 μm wide) bears 21 pairs of setae which, with the exception of the short *z1, s1, s2* and *r2*, are all finely pilose and of unusually even length and thickness. However, *j4, z5* and *r3* are actually the longest. The opisthonotal shield (276–324 μm long × 400–492 μm wide) bears 13 pairs of setae of even length and the posterior membrane another eight or more similar pairs.

The tritosternum is typical with a narrow base and pilose laciniae. It is flanked by a pair of small v-shaped presternal shields. The sternal shield (283–348 μm long) shows little variation. It is reticulated and the setae are simple (Fig. 19B). The anal shield is oval and reticulated and the three anal setae are simple. Some of the opisthogastric setae are finely pilose. Small circular and granular metapodal shields are present and the peritreme extends to the level of coxa I.

The tectum is trispinate but in two forms, that of the future male (Fig. 19C) and female (Fig. 19D). Oudemans (1914, Heft 8, Taf. III) figures three variations in the male form in which the modified central prong is variously developed, but I have not noted that this variation is so clear cut as to warrant individual attention. Indeed the variation in outline of the tectum in many species is quite extensive. The chelicera is shown in figure 19E and the palp trochanter, femur and genu in figure 19F. The venter of the gnathosoma is as in figure 19G: the palpcoxal setae only appear to be finely pilose. The leg setae show no characteristic formations, although there is one stout seta ventrally on genu II.

MALE. The dorsum (1260–1420 μm long × 756–900 μm wide) is strongly sclerotized and entirely reticulated and has a transverse suture medially (Fig. 19H). The podonotal region bears 23 pairs of setae, *r4* being often ventrally situated in mounted specimens. Setae *r3* are the only ones that are conspicuously long, although most are, to some extent, finely pilose. The opisthonotal region bears up to about 26 pairs of setae which are, in general, slightly shorter than the podonotals, but like them are largely pilose.

The tritosternum has a short narrow base and pilose laciniae. It is flanked by granular presternal shields. The genital lamina often protrudes from the sternal shield (Fig. 19I). The ventral sclerotization is reticulated and all setae are fine and slender, some in the

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Fig. 19 *Parasitus loricatus* (Wankel), **deutonymph** – A dorsum; B sternal shield; C tectum of male deutonymph; D tectum of female deutonymph; E chelicera; F palp trochanter, femur and genu; G venter of gnathosoma: **male** – H dorsum; I venter; J tectum; K chelicera; L palp femur and genu; M venter of gnathosoma; N leg II; O right tarsus of leg II (excluding the ambulacrum) of a Devon specimen (see text, p. 286).

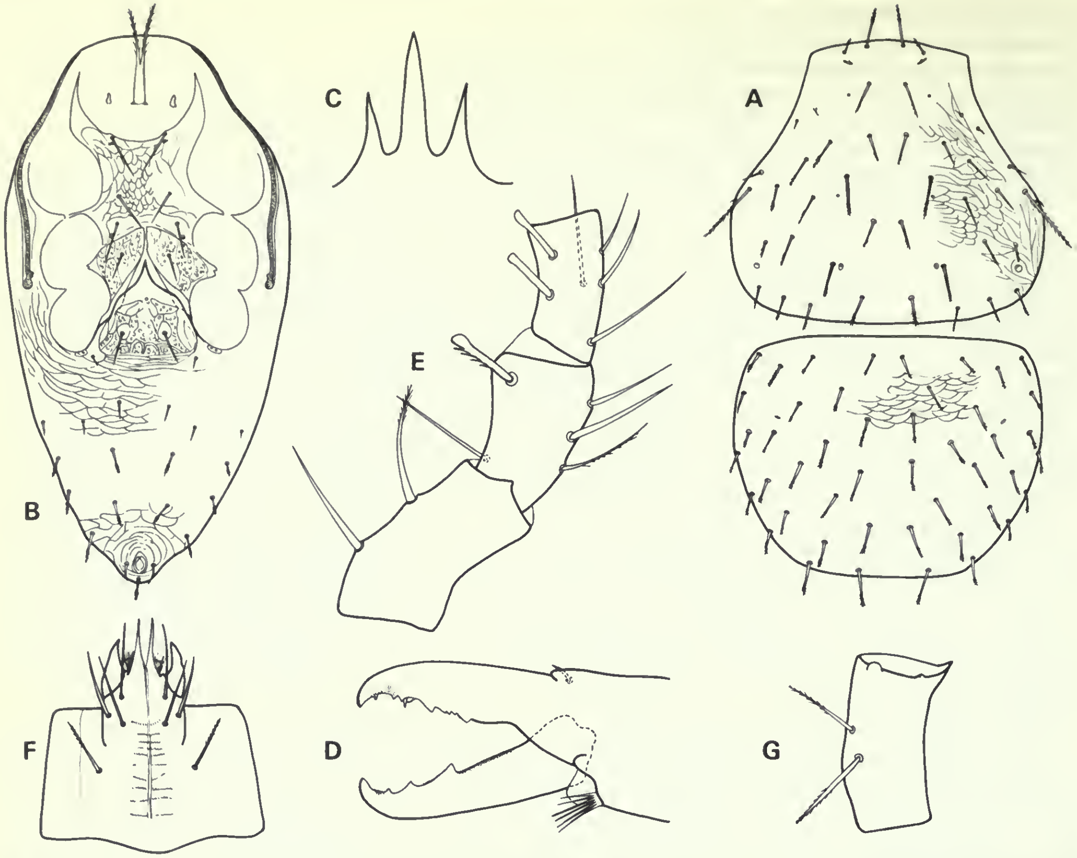

Fig. 20 *Parasitus loricatus* (Wankel), **female** – A dorsal shields; B ventral sclerotization; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma; G coxa of leg I.

opisthogastric region being finely pilose. The paranal setae appear simple whilst the postanal is slightly stouter and finely pilose. The peritreme extends anteriorly to coxa I.

The tectum is shown in figure 19J, with variation dotted. The correlation between the tectum in the male deutonymph and adult is clear. The chelicera is shown in figure 19K. The fixed digit bears a ridge of at least 16 very small teeth and the movable digit one large tooth only. The chaetotaxy of the palp femur and genu is as in figure 19L. The stalked corniculi are strongly cleft, the inner portion being rounded, the outer pointed (Fig. 19M). The gnathosomal setae are slender. Leg II is shown in detail in figure 19N. The accessory spur on the femur is strongly bifid, whilst the tarsus is curved to a varying degree. Figure 19O shows the right tarsus II (excluding the ambulacrum) of the specimen from Devon recorded by Turk & Turk (1952) as *Parasitellus ferox*.

Female. The dorsal shields are completely reticulated and the chaetotaxy is similar to that of the male. Both shields tend to readily flatten out to their maximum width on clearing and these measurements are given. The podonotal shield (636–768 μm long × 624–840 μm wide) bears 23 pairs of setae most of which are pilose (Fig. 20A). The opisthonotal shield (544–648 μm long × 624–840 μm wide) also bears 23 pairs of setae which, as in the male, are slightly shorter than those on the podonotal shield.

The tritosternum has a narrow base and pilose laciniae. The sternal shield is reticulated with a conspicuous pattern and the sclerotization extends laterally and forwards around coxae I (Fig. 20B). The presternal shields are small and crescent shaped. The metasternal and genital shields are reticulated and are conspicuously ornamented. The sternogenital setae are simple. The opisthogastric region is entirely reticulated and bears nine pairs of setae, some of which appear finely pilose distally, whilst the surrounding membrane has mainly very short setae. The paranal setae are simple, the postanal pilose distally. The peritreme extends to coxa I.

The tectum is boldly trispinate with the centre tine the longest (Fig. 20C), and is clearly correlated with that of the female deutonymph. The chelicera is shown in figure 20D. The inner edge of the movable digit has a conspicuous file-like pattern and the fixed digit has a similar area between the second and third teeth from the tip, a condition that I do not recall seeing in any other species of Parasitinae. The chaetotaxy of the palp trochanter, femur and genu is shown in figure 20E. The corniculi are strong and the gnathosomal setae are of approximately equal length (Fig. 20F). The leg setae are mainly slender and many are finely pilose. Leg II bears a single stout ventral seta on the femur, genu, tibia and tarsus, and on leg III similar setae are present, although on the genu and tibia these are paired. Leg IV bears a single stout ventral seta on each segment from trochanter to tibia. Coxa I bears a tooth on the inner distal margin (Fig. 20G).

MATERIAL EXAMINED. 130 samples – 174 DNN, 86 ♂♂, 142 ♀♀.
ENGLAND: Isles of Scilly, Devon, Somerset, Hampshire, Gloucestershire, Wiltshire, Berkshire, Oxfordshire, Middlesex, Hertfordshire, London, Essex, Kent, Surrey, Suffolk, Cambridgeshire, Huntingdonshire, Worcestershire, Staffordshire, Lincolnshire, Derbyshire, Cheshire, Manchester, Cumberland, Yorkshire, Northumberland, Durham.
WALES: Breconshire.
SCOTLAND: Roxburghshire, Midlothian, West Lothian, Argyllshire (Lismore, Shuna), Inner Hebrides (Scalpay), Outer Hebrides (Lewis).
IRELAND: Cork, Meath.

This widespread European species is distributed throughout the British Isles. Its favoured habitats are, like several other *Parasitus,* compost and dung heaps, rotting vegetation, mushroom beds, small mammal nests (especially voles, moles and shrews), birds' nests in burrows or holes in trees, and in caves. Additionally, situations such as on house-mouse and brown rat, wasp and bumblebee are recorded. I have examined only four samples from leaf-litter where there was no obvious host in the immediate vicinity (Isles of Scilly and Staffordshire). Abroad it is recorded from similar habitats and Karg (1971) notes that it is scarce in arable soil although a few such records are quoted by Micherdzinski (1969).

DISTRIBUTION. Previous British records are from Yorkshire and Lancashire (*anglicus*) and Middlesex and Scotland (Hull, 1918), Berkshire* (Elton *et al.,* 1931), Somerset** (Turk, 1944), Devon (Turk & Turk, 1952, misidentified as *Parasitellus ferox* (Träg.)), Buckingham Palace Gardens, London (Bristowe, 1964), Cambridgeshire, Worcestershire and Wigtownshire (Mead-Briggs & Hughes, 1966), Huntingdonshire (Davis, 1970), and Yorkshire, Devonshire and Breconshire (Turk, 1972). Turk (1967) lists this species as a cave inhabitant without citing localities. In the same paper he also cites *Parasitellus ferox* (Trägårdh), which presumably refers to the Devon material referred to above (Turk & Turk, 1952). Other cave records are Devon (Hazelton, 1967*a*, *b*, 1970*a*), Somerset (Hazelton, 1967*a, c,* 1968*a, c*), Wiltshire (Hazelton, 1971*b*), Breconshire (Hazelton, 1971*a, b*), Derbyshire (Hazelton, 1972), Cumberland (Hazelton, 1967*a,* 1972) and Yorkshire (Hazelton, 1970, 1972). The mention by Micherdzinski (1969) of this species being recorded, as *Gamasus crassus* Kramer, from the London area by Michael (1892) is based on his erroneus translation of Michael's introductory remarks. The specimens in question were from Switzerland.

*A single slide in the Museum Collection of a male deutonymph of this species from a dead bank-vole *Clethrionomys glareolus* (Schreber), Bagley Wood, Berkshire, 8 February, 1926, and identified by Vitzthum as '*Parasitus spinipes* Koch' is most probably part at least of the material forming the record by Elton *et al.* (1931) of '*Parasitus spinipes* Oudemans'. A second slide, bearing the same habitat data, but identified by Vitzthum as *Eugamasus magnus* Kramer, is of a male deutonymph of *P. loricatus,* collected on 10 December, 1925.

**Micherdzinski (1969) misquotes Turk (1944) and cites the Mendip Hills as being in Derbyshire.

When Hull (1918) described *Gamasus anglicus* from Yorkshire (W. Falconer) and Lancashire (Rev. S. G. Birks) he listed *Gamasus loricatus* Wankel as 'A species unknown to me'. Nevertheless, his figures of *anglicus*, and especially leg II of the male, leave no doubt that the new species is synonymous with *loricatus* and it is treated as such by Micherdzinski (1969). I have examined a single male from Brantingham Dale, Brough, Yorkshire, 11 April 1916, in the Falconer Collection at Liverpool Museum, and this is probably the material upon which Hull based his record. However, the specimen is *Euryparasitus emarginatus* (C. L. Koch), family Rhodacaridae, and it is clear from the label that this was its original identification under the junior synonym of *Euryparasitus terribilis* (Michael). But, the original identification has been crossed out and '♂ *Gamasus anglicus*' inserted in either Hull's or Falconer's writing. Hull's record from Lancashire almost certainly refers to a sample (1 ♂, 2 ♀♀ and 5 DNN) in the Hull Collection from Holy Trinity Churchyard, Darwen, Lancashire, 6 January 1916, S. G. Brade-Birks coll., and these specimens are *Parasitus loricatus*.

Parasitus loricatus is recorded from the Faeroes (Trägårdh, 1931), Iceland (Sellnick, 1940), Sweden (Lundqvist, 1974), Finland (Nordberg, 1936), Holland (Oudemans, 1914), Belgium (Willmann, 1935, Leruth, 1939, van Daele & Heungens, 1974), France (Bonnet, 1911, Trägårdh, 1912, Cooreman, 1959), Germany (Kramer, 1876, Oudemans, 1930*b*, Willmann, 1932*a*, 1937, 1938*b*, 1952, Karg, 1965, 1971, Holzmann, 1969), Spain (Trägårdh, 1912), Austria (Franz, 1943), Switzerland (Cooreman, 1959, Schweizer, 1922, 1949, 1961), Italy (Cooreman, 1959), Poland (Pax & Maschke, 1935, Willmann, 1936*a*, Kielczewski, 1957, Micherdzinski, 1969), Czechoslovakia (formerly Austria, Wankel, 1861; Pax & Maschke, 1935, Maschke, 1936, Willmann, 1954), Jugoslavia (Willmann, 1932*b*), Romania (Coorman, 1951*b*), U.S.S.R. (Pinchuk, 1976), Western Siberia (Davydova, 1969, 1976) and Morocco (Cooreman, 1951*a*).

Parasitus mustelarum Oudemans
(Fig. 21A–P)

Parasitus mustelarum Oudemans, 1902*b*: 9, 33 *nomen nudum*; 1903*b*: 85; 1905*a*: 78; 1912*c*: 260. Karg, 1965: 232, 239, 245; 1971: 448. Micherdzinski, 1969: 444.
Parasitus (Coleogamasus) mustelarum: Tichomirov, 1969: 1476. Bregetova *et al.*, 1977: 85, 91.
Gamasus coleoptratorum L.: Berlese, 1882*c*: 120 ('tritonymph').
Gamasus intermedius Berlese, 1904*a*: 240. Micherdzinski, 1969: 450.
Gamasus (Gamasus) intermedius: Berlese, 1906: 152.
Eugamasus intermedius: Holzmann, 1969: 14.

Berlese (1906), Oudemans (1912*c*), Holzmann (1969) and Karg (1971) all consider *intermedius* Berlese to be synonymous with *mustelarum* Oudemans, whilst Micherdzinski (1969) feels that they are distinct species, being differentiated above all on the form of the tectum. I have examined specimens of *mustelarum* in the Oudemans collection and consider the British material documented here to be conspecific with it. Berlese (1906) considered *intermedius* to have priority over *mustelarum* but he overlooked Oudemans's (1903*b*) description of the deutonymph of *mustelarum*, as has already been pointed out by Oudemans (1912*c*).

DEUTONYMPH. The forty specimens examined in the present study show the least variation of any species or developmental form. The dorsum is entirely covered by two moderate to strongly sclerotized reticulated shields whose chaetotaxy is shown in figure 21A. The podonotal shield (420–444 μm long × 420–456 μm wide) bears 20 pairs of setae, *s2* being situated off the shield. The majority of setae are short and rather spinose, but four pairs are conspicuously longer. Setae *r3* are the longest and are pilose for most of their length, whilst *z5* are almost as long and are pilose in their distal halves. Setae *j1* and *j4* are also longer than the majority and are pilose distally. The opisthonotal shield (276–288 μm long × 360–396 μm wide) bears 17 pairs of setae of which one pair only, *Z3*, are stout and pilose distally.

The tritosternum has a narrow base and pilose laciniae. It is flanked by wide shallow presternal shields. The strongly sclerotized sternal shield (360–396 μm long) is of

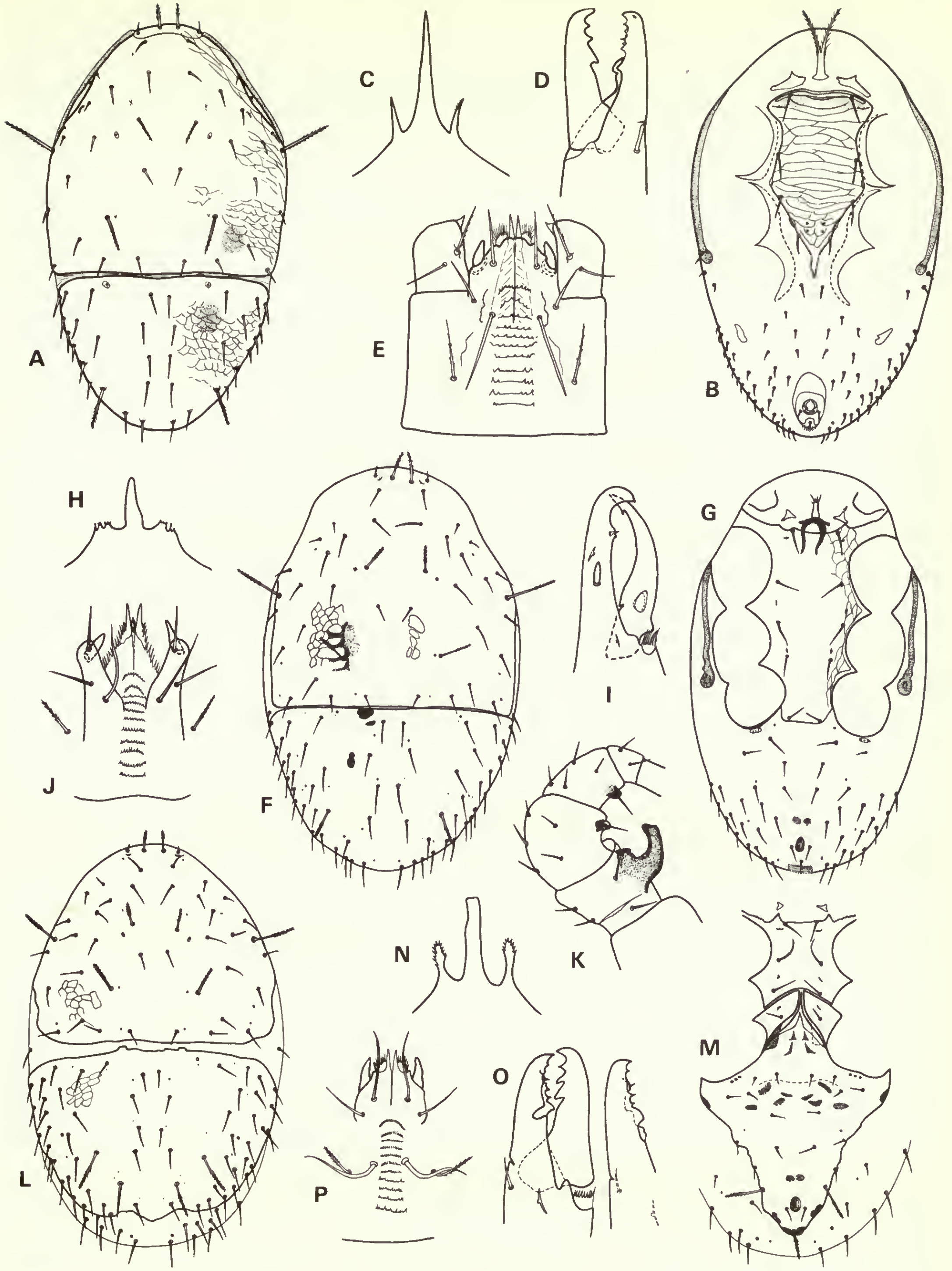

Fig. 21 *Parasitus mustelarum* Oudemans, **deutonymph** – A dorsum; B venter; C tectum; D chelicera; E venter of gnathosoma: **male** – F dorsum; G venter; H tectum; I chelicera; J venter of gnathosoma; K armature of leg II: **female** – L dorsum; M ventral sclerotization; N tectum; O chelicera; P venter of gnathosoma. F–P after Holzmann, 1969.

characteristic outline and is attenuated posteriorly between coxae IV. A narrow transverse strip passing through sternal setae I is weakly sclerotized (Fig. 21B). The sternal setae become progressively shorter from I–IV and the opisthogastric setae, which number approximately 31 pairs, are shorter still. The anal shield is elliptical with the three setae short and simple. The peritreme extends to coxa I.

The tectum is as in figure 21C. The centre prong is often broken short. The chelicera is shown in figure 21D, and the venter of the gnathosoma and the palp trochanter in figure 21E. The anterolateral seta on the palp femur is simple and tapered, whilst those of the palp genu are flattened distally. All leg setae are rather short and spinelike and some are finely pilose distally.

MALE AND FEMALE. So far the adults have not been collected in the British Isles. Figures 21F–K of the male and 21L–P of the female are based on Holzmann (1969). The idiosoma of the male measures *c.* 900 μm long × 480 μm wide, and the female 900–990 μm long × 560–635 μm wide.

MATERIAL EXAMINED. 12 samples – 40 DNN.

ENGLAND: Isles of Scilly, Dorset, Hampshire, Norfolk, Worcestershire, Yorkshire.

With the exception of three deutonymphs that were found on piglets in Norfolk and Yorkshire, all the material examined is from beetles, viz.: *Geotrupes spiniger* (Marsham) and *stercorarius* (L.), *Aphodius* sp. and ?*Colobopterus fossor* (L.).

DISTRIBUTION. The only previous British record of this species is from *Geotrupes stercorarius* at Wareham, Dorset, 7 October 1958 (Hyatt, 1959) (*'Parasitus* nr. *intermedius'*). The females recorded from Cheshire as *Parasitus intermedius* (Berlese) by Turk & Turk (1952) are *Vulgarogamasus kraepelini.*

It is recorded from Norway (Berlese, 1906), Holland (Oudemans, 1902*b*), Germany (Holzmann, 1969, Micherdzinski, 1969, Karg, 1971), Austria (Leitner, 1946), Poland (Micherdzinski, 1969), Switzerland (Schweizer, 1949), Italy (Berlese, 1906) and Western Siberia (Davydova, 1976). Habitats are beetles, straw, dung, compost, fungi and occasionally associated with small mammals.

The species referred to as *Parasitus cf. intermedius* by Costa (1966) is not conspecific with *P. mustelarum.*

Genus *VULGAROGAMASUS* Tichomirov

Vulgarogamasus Tichomirov, 1969. *Zool. Zh.* **48:** 1335.

TYPE SPECIES. *Parasitus burchanensis* Oudemans, 1903*b*.

Dorsal shield of male entire, with transverse suture; female and deutonymph with separate podonotal and opisthonotal shields. Setae of dorsal hexagon very similar in form and length, deutonymphs with *z5* sometimes clearly the longest. Tritosternum normal, biramous. Junction between sternal and metasternal shields of female oblique. Genital shield of female triangular or subtriangular. Opisthogaster with rarely more than 26 pairs of setae. Seta *al* of palp femur multifid or pectinate or scalloped distally; setae al_1 and al_2 of palp genu entire, spatulate. Male chelicerae symmetrical. Corniculi short, entire. Legs of deutonymph and female without spurs; only leg II of male spurred. Lobes of pulvilli normal, rounded.

Vulgarogamasus burchanensis (Oudemans)
(Figs 22A–H; 23A–G)

Parasitus burchanensis Oudemans, 1903*b*: 86; 1905*a*: 80. Berlese, 1906: 134. Sellnick, 1940: 51. Micherdzinski, 1969: 565. Karg, 1971: 449. Type examined.

Parasitus (Vulgarogamasus) burchanensis: Tichomirov, 1969: 1335, 1476. Bregetova *et al.*, 1977: 80, 81.

Vulgarogamasus burchanensis: Evans & Till, 1979: 210.

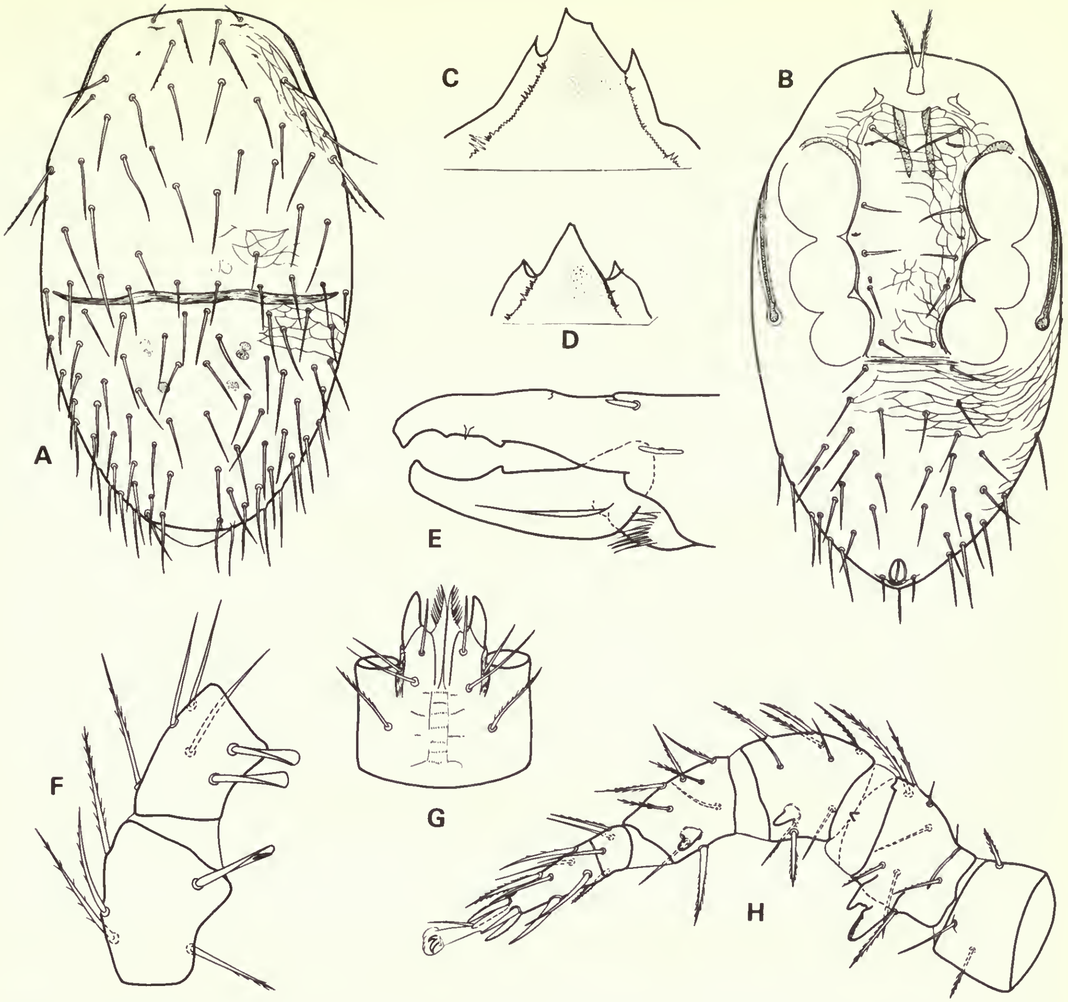

Fig. 22 *Vulgarogamasus burchanensis* (Oudemans), **male** – A dorsum; B venter; C, D tectum; E chelicera; F palp femur and genu; G venter of gnathosoma; H leg II.

Eugamasus butleri Hughes, A. M., 1948: 121; 1961: 207; 1976: 350. Hughes, T. E., 1959: 150. Micherdzinski, 1969: 551. Tichomirov, 1969: 1335. Type examined.

Eugamasus butleri Hughes has been synonymized with *Parasitus burchanensis* Oudemans by Tichomirov (1969) in the course of designating *burchanensis* as the type of his new subgenus *Vulgarogamasus.* I have examined Oudemans's type male and agree that it is synonymous with syntype males of *butleri.* The female figured and identified as *burchanensis* by Sellnick (1940) is considered here to be conspecific with the syntype female of *butleri.*

Deutonymph. Unknown.

Male. The dorsums of two syntype males of *Eugamasus butleri* measure 680–700 μm long × 430–440 μm wide and are entirely sclerotized and reticulated and each is divided by a median transverse suture (Fig. 22A). The podonotal region bears 23 pairs of setae although in the specimen figured the left *r2* is missing. All setae are slender and several are finely pilose on one margin, and *r3* are scarcely longer than the majority. The opisthonotal region bears about 35 pairs of longish slender setae.

The tritosternum has a narrow base and pilose laciniae. It is flanked by elongate presternal shields (Fig. 22B). The sternogenital and opisthogastric regions are well sclerotized and reticulated and all setae are fine and simple. The postanal seta is finely pilose and is slightly longer than the paranals. The peritreme extends to coxa I.

The tectum comprises a broadly triangular plate, sometimes irregularly formed, with a pair of lateral teeth. Additionally two diverging rows of fine sawlike teeth run back from the basal angles of the centre prong. Its surface is granular (Figs 22C, D). The chelicera is as in figure 22E. The chaetotaxy of the palp femur and genu is shown in figure 22F, and the venter of the gnathosoma in figure 22G. The palpcoxal setae are pilose, the hypostomatics simple. Legs I, III and IV bear mainly simple setae, those on the posterior legs being stoutest. Leg II is shown in figure 22H.

FEMALE. The podonotal shield of the single syntype female of *Eugamasus butleri* examined measures 372 μm long × 396 μm wide (Fig. 23A). It is finely granular and lightly reticulated and bears 22 pairs of setae of which *j1* are finely pilose and some others scarcely so. Setae *r3* are the longest but only slightly. The opisthonotal shield measures 312 μm long × 408 μm wide, is finely granular and lightly reticulated. It bears 26 simple setae on the left side and 27 on the right. The posterior membrane bears 9 or 10 pairs of setae of similar length which show slight pilosity.

The tritosternum has a narrow base and pilose laciniae. Contiguous with its base is a pair of fragmentary presternal shields and more laterally the main presternal shields (Fig. 23B). Sternal setae I lie on an area of reticulation which is more weakly sclerotized than the main part of the sternal shield. The sternal, metasternal and genital shields are granular, the setae fine and simple. The main part of the endogynium is circular and sac-like. The opisthogastric shield is irregular in outline and the anal region is almost separated. The opisthogastric setae are simple whilst the postanal seta is slightly longer than the paranals. The metapodal shields are represented by small granular circles. The peritreme extends to coxa I.

The tectum is shown in figure 23C, the chelicera in figure 23D, the palp trochanter, femur and genu in figure 23E, and the venter of the gnathosoma in figure 23F. The leg setae do not appear to exhibit any peculiarities. In the syntype examined femur II has a pronounced sclerotized ridge anterodorsally (Fig. 23G), but this is not present in the specimen from Lanarkshire.

MATERIAL EXAMINED. 2 samples – 2 ♂♂, 2 ♀♀.
SCOTLAND: One female from deep litter in a poultry-house, Lanarkshire, 1977.
IRELAND: Two males and one female from the syntype series of *Eugamasus butleri* in floor sievings from brewers' grain, Belfast.

DISTRIBUTION. Other British records (as *E. butleri*) are from poultry litter in Cambridgeshire (Brady, 1970 and pers. comm.) and from farms, flour mills and railway wagons in the Republic of Ireland (no precise localities) (Cusack, Evans & Brennan, 1975).

It has been recorded from the German North Sea island of Borkum (Oudemans, 1903*b*, 1905*a*) (no habitat given) and from Iceland (Sellnick, 1940) in a barn/granary ('Scheune') and in dry grass and old hay.

Vulgarogamasus immanis (Berlese)
(Figs 24A–O; 25A–G)

Gamasus (Eugamasus) immanis Berlese, 1904*a*: 262; 1906: 179.
Eugamasus immanis: Sellnick, 1940: 49.
Parasitus immanis: Micherdzinski, 1969: 515. Karg, 1971: 446.
Parasitus (Vulgarogamasus) immanis: Tichomirov, 1969: 1336, 1476. Bregetova *et al.*, 1977: 80, 81.
Vulgarogamasus immanis: Evans & Till, 1979: 210.

DEUTONYMPH. The dorsal shields are considerably smaller than the idiosoma and are entirely covered by a pattern of small reticulation and areas of fine granulation (Fig. 24A).

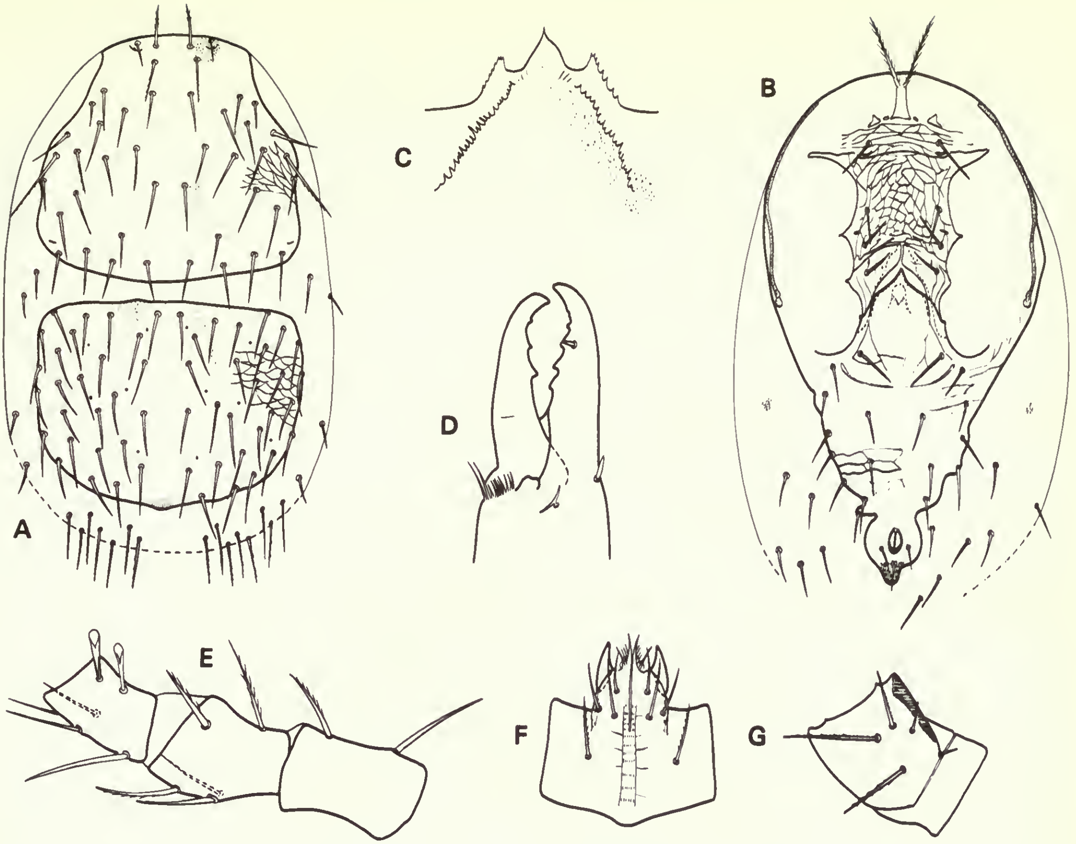

Fig. 23 *Vulgarogamasus burchanensis* (Oudemans), **female** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma; G femur of leg II.

The podonotal shield (830–880 μm long × 630–700 μm wide) bears, in the specimens examined, from 15–17 pairs of setae. In the figured specimen the left side has 17 setae and the right side has 15. In other specimens, one or more of the lateral setae are located on a piece of shield that is almost separated from the margin but has clearly not been damaged. Setae *r3* (*c.* 270 μm) are the longest and are situated on small granular plates separate from the podonotal shield, whilst *z5* (*c.* 160 μm) are only slightly longer than the remainder which range from *c.* 100–150 μm. All setae are simple. The opisthonotal shield (500–550 μm long × 480–550 μm wide) bears from 11–15 pairs of setae which are often unpaired on the posterior margin. The figured specimen bears 13 pairs. The surrounding membrane bears setae of similar lengths.

The tritosternum has a narrow base and pilose laciniae, and the presternal shields are small and triangular. The reticulated sternal shield is of somewhat irregular but characteristic outline (Fig. 24B), and ranges from 510–540 μm in length. The opisthogastric setae are simple and small granular metapodal shields are present. The reticulated anal shield varies rather in outline but always carries an additional pair of setae towards its anterior margin. The postanal seta is longer than the paranals. The peritreme does not quite reach coxa I.

The tectum is denticulate and of a constant general form comprising a central elongate area and two strongly denticulate lateral areas, but there is frequent variation, especially in the form of the central area (Figs 24C, D). The chelicera is shown in figure 24E. The digits are slender and the movable measures *c.* 275 μm. The palp trochanter, femur and genu are shown in figure 24F. The gnathosomal setae are slender and simple and sixteen or more rows

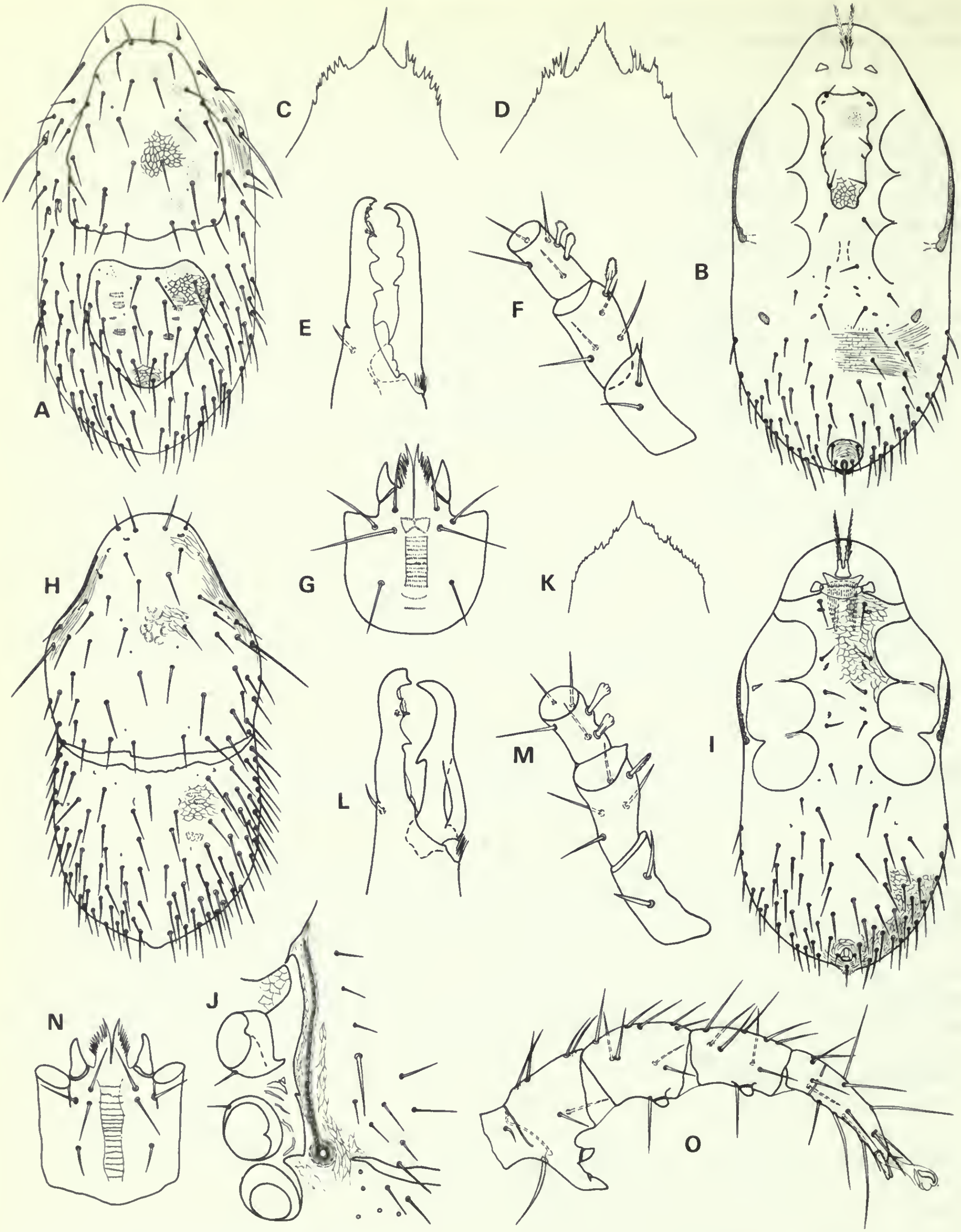

Fig. 24 *Vulgarogamasus immanis* (Berlese), **deutonymph** – A dorsum; B venter; C, D tectum; E chelicera; F palp trochanter, femur and genu; G venter of gnathosoma: **male** – H dorsum; I venter; J peritreme in detail; K tectum; L chelicera; M palp trochanter, femur and genu; N venter of gnathosoma; O leg II.

of hypognathal denticles are present. The corniculi are strong and smooth (Fig. 24G). The leg setae are all slender and tarsus IV bears dorsally two conspicuously long setae measuring *c.* 350–400 μm.

MALE. The dorsum is entire and averages 2160–2250 μm long × 1110–1130 μm wide. It is strongly sclerotized, finely reticulated and with a broad transverse suture (Fig. 24H). The podonotal region bears about 25 pairs of simple setae not arranged entirely symmetrically. Seta *s1* at least may not be paired (as in the figured specimen), and the longest setae are *r3* (*c.* 300 μm). The opisthonotal region bears over 40 pairs of setae, but here again they are neither entirely symmetrically arranged nor paired.

The tritosternum has a rather short narrow base which appears to be extensile, and pilose laciniae (Fig. 24I). A pair of small presternal shields is present. The entire venter is very strongly sclerotized and finely reticulated. The setae are slender and simple. The postanal seta is longer than the paranals. The peritreme extends almost to coxa I and is shown in detail in figure 24J.

The tectum is shown in figure 24K. Variation noted is in the form of the denticulations, but the general theme is constant. The chelicera is shown in figure 24L. The movable digit measures *c.* 310 μm. The chaetotaxy of the palp trochanter, femur and genu is as in figure 24M. The corniculi taper and are divergent and the gnathosomal setae are slender (Fig. 24N). The leg setae are simple and slender and tarsus IV bears dorsally two conspicuously long setae measuring *c.* 360 μm each. Leg II is shown in detail in figure 24O.

FEMALE. The podonotal shield (1270–1340 μm long × 1110–1210 μm wide) is strongly sclerotized and granular and with conspicuous areas of circular punctations (Fig. 25A). It bears 23 pairs of simple setae of which the longest are *j4* (160 μm) and *r3* (*c.* 240 μm) and their arrangement is more symmetrical than in either the deutonymph or the male. The opisthonotal shield (840–1010 μm long × 970–1050 μm wide) is of similar form to the podonotal and bears 22 pairs of simple setae. The surrounding membrane bears slightly shorter setae.

The tritosternum has a short narrow base and pilose laciniae. It is flanked by a pair of conspicuous presternal shields (Fig. 25B). The sternal shield is granular and entirely reticulated, but its anterior margin is indistinct. The genital shield is triangular and granulate. Figure 25C shows the genital region in greater detail. The opisthogastric shield is strongly granulate on the surface with reticulations below. Its margin is irregular in places and the anal region is almost cut off. In the specimen figured one of the adjacent short interscutal setae is on a small granular plate and a second seta lies on a narrow granular strip close to the anus. The three anal setae are of almost equal length. The peritreme does not reach coxa I.

The tectum is basically of the same form as in the deutonymph and male, but in the figured specimen the denticulations are less developed or even broken off (Fig. 25D). The chelicera (Fig. 25E) is again long and slender and the movable digit measures *c.* 400 μm. The palp trochanter, femur and genu are shown in figure 25F, and the venter of the gnathosoma in figure 25G. The corniculi are shaped as in the male and are very slightly divergent. The gnathosomal setae are simple. All leg setae are simple and tarsus IV bears dorsally at least two setae measuring *c.* 300 μm.

MATERIAL EXAMINED. 4 samples – 7 DNN, 8 ♂♂, 3 ♀♀.

ENGLAND: One male from Ringstead Bay, Dorset, 1 November 1911, coll. H. St. J. K. Donisthorpe.

SCOTLAND: One male and one female from the Edinburgh district (Firth of Forth), 1905, coll. Wm. Evans.

WALES: Seven deutonymphs, six males and two females from seaweed on the shore of the Menai Straits, Caernarvonshire, 23 August 1976, coll. Mrs M. J. Morgan.

DISTRIBUTION. The first published British record of this species is that of Berlese (1906) who examined two specimens from Ireland sent to him by Halbert. King (1912) recorded it from

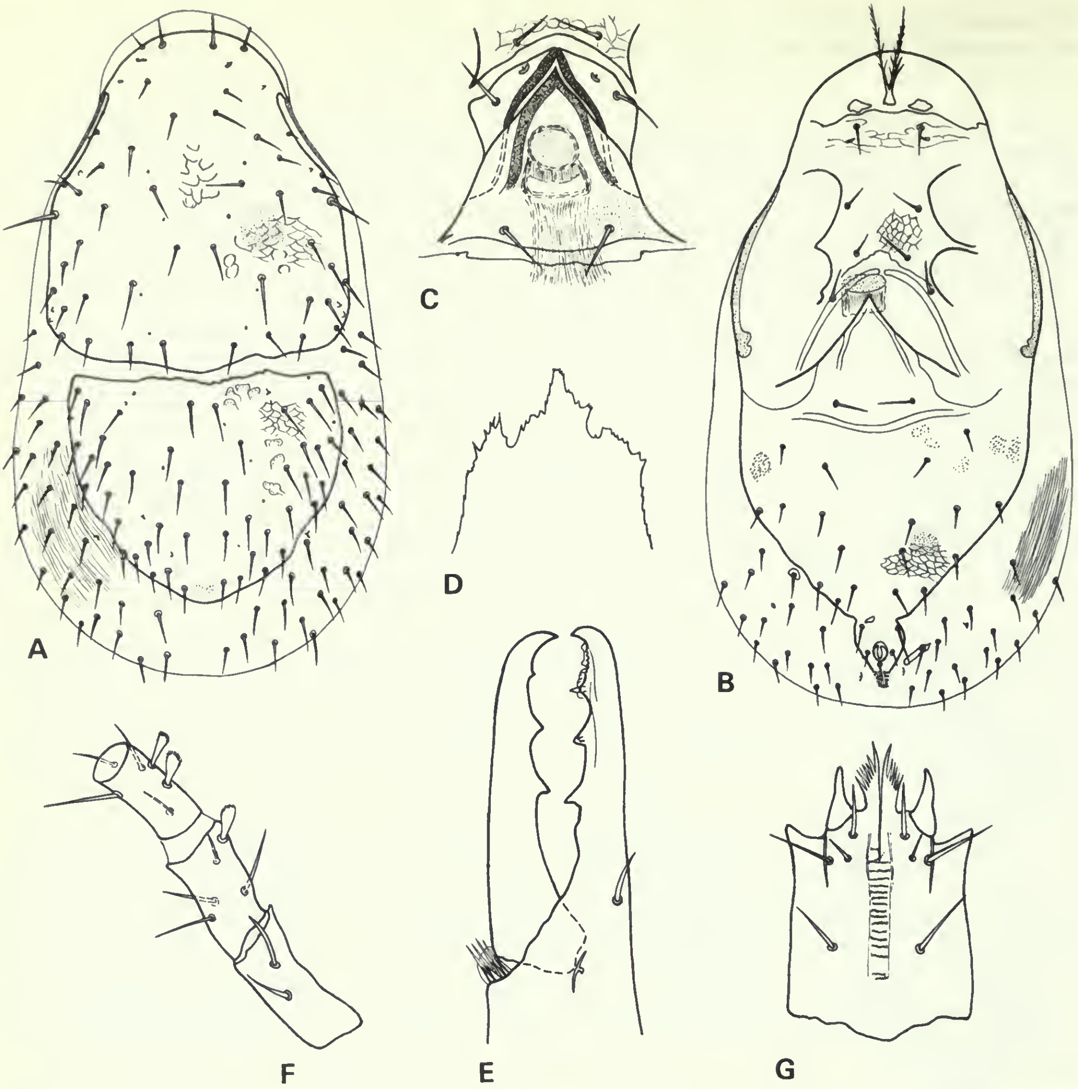

Fig. 25 *Vulgarogamasus immanis* (Berlese), **female** – A dorsum; B venter; C genital region; D tectum; E chelicera; F palp trochanter, femur and genu; G venter of gnathosoma.

the Firth of Clyde and later (King, 1914), whilst recording it additionally from Dunbartonshire, he described in some detail his field and laboratory observations on specimens obtained in the Firth of Clyde. In his 1914 paper King referred to Berlese's (1906) Irish record as 'Iceland'. This had already been referred to by Sellnick (1940: 50) and is explained by the fact that Berlese wrote *'duasque in* "Islanda", (*quas mihi misit cl. Halbert*)'. Berlese made a similar statement when he described the oribatid mite *Lohmannia insignis* (Berlese, 1904*c*: 23) as '*Hibernia collecta*' and wrote on at least one of Halbert's labels '*Lohmannia insignis* Berl. Islanda'. Subsequent British records are from Co. Mayo, Co. Cork and Co. Dublin (Halbert, 1915), Co. Galway (Halbert, 1920) and Northumberland and Lancashire (Hull, 1918).

It is recorded from Iceland (Sellnick, 1928, 1940) and Norway (Berlese, 1904*b*).

The sparsity of records of this species is at first surprising in view of its size. I had not seen fresh material amongst the quite numerous samples examined from seashore debris until Mrs

M. J. Morgan collected some specimens from seaweed in the Menai Straits. Although Halbert (1920) and King (1914) also found specimens under decaying seaweed, I feel that Halbert's (1915, 1920) comments that it is found under stones and shingle allude most probably to the more usual habitat of this large species which in all probability is a widely distributed and common member of the seashore community. It is interesting to note that it was not recorded by Glynne-Williams & Hobart (1952) in their study of seashore crevice fauna on Anglesey.

Vulgarogamasus kraepelini (Berlese) comb. nov.

(Figs 26A–M; 27A–G)

Gamasus (Eugamasus) Kraepelini Berlese, 1905: 232; 1906: 170.
Gamasus kraepelini: Hull, 1918: 85.
Eugamasus kraepelini: Schweizer, 1961: 21. Holzmann, 1969: 8.
Parasitus kraepelini: Micherdzinski, 1969: 573. Karg, 1971: 450.
Parasitus intermedius (Berlese, 1882 *sic*) sensu Turk & Turk, 1952: 478, non Berlese, 1904*a* = *P. mustelarum* Oudemans, 1902*b*.
Parasitus (Eugamasus) kraepelini: Tichomirov, 1969: 1475. Bregetova *et al.*, 1977: 63, 69.
Paracarpais (Aceocarpais) kraepelini: Athias-Henriot, 1978: 48

I have examined Schweizer's types of both *Eugamasus zschokkei* (1922) and *Eugamasus zschokkei* var. *fturi* (1949), but unlike Micherdzinski (1969) I do not consider the latter to be synonymous with *kraepelini*. Both *zschokkei* and *fturi* are similar to *kraepelini*, but are not conspecific with any of the known British species.

DEUTONYMPH. The podonotal shield (370–450 μm long × 440–470 μm wide) is entirely reticulated and bears 20 pairs of fine slender setae (Fig. 26A). Setae *s2* are off the shield, and *z5* and *r3* are the longest and show fine traces of pilosity. In the specimen figured the right *s6* is off the shield. The opisthonotal shield (260–290 μm long × 400–410 μm wide) is entirely reticulated. It bears 13 pairs of fine simple setae which increase in length posteriorly. Some show fine pilosity. The setae on the posterior membrane are similar.

The tritosternum has a narrow base and pilose laciniae. It is flanked by small squarish or rectangular presternal shields. The sternal shield (260–290 μm long) appears to be consistently rounded, concave anteriorly and with a regular outline (Fig. 26B). All sternal and opisthogastric setae are fine and slender. The anal shield is broadly oval and reticulated with the postanal seta twice the length of the paranals. The metapodal shields are generally present although indistinct, and the peritreme extends to coxa I.

The tectum comprises three prongs, generally of even length, with the outer two being the more slender, but the centre one may be short (Figs 26C, D). The chelicera is shown in figure 26E, the chaetotaxy of the palp trochanter, femur and genu in figure 26F, and the venter of the gnathosoma in figure 26G. The leg setae are slender and on legs II–IV many are finely pilose. Genu IV bears a strong curved pilose dorsal seta distally. The longest seta on tarsus IV measures *c.* 215 μm.

MALE. The idiosoma is strongly sclerotized and measures 840–864 μm long × 492–592 μm wide. The dorsum is divided by a median transverse suture and the two halves may overlap (Fig. 26H). The podonotal region bears 21–22 pairs of setae which are mainly without traces of pilosity, although *j1, j4* and *r3* are generally finely pilose. A short seta external to *s6* is not always on the dorsal surface. The opisthonotal region bears no conspicuously long setae although some posteriorly are stouter than the majority and a number show fine pilosity.

The tritosternum has a narrow base and pilose laciniae. It is flanked by a pair of small right-angled to squarish presternal shields (Fig. 26I). Sternal setae I, which appear finely pilose, are situated off the sclerotized holoventral area on to a granular strip flanking the genital lamina. The postanal seta is one and a half times as long as the paranals, but considerably stouter and also finely pilose. The peritreme extends to coxa I.

The tectum is uniquely shaped and shows little variation (Fig. 26J). The chelicera is shown

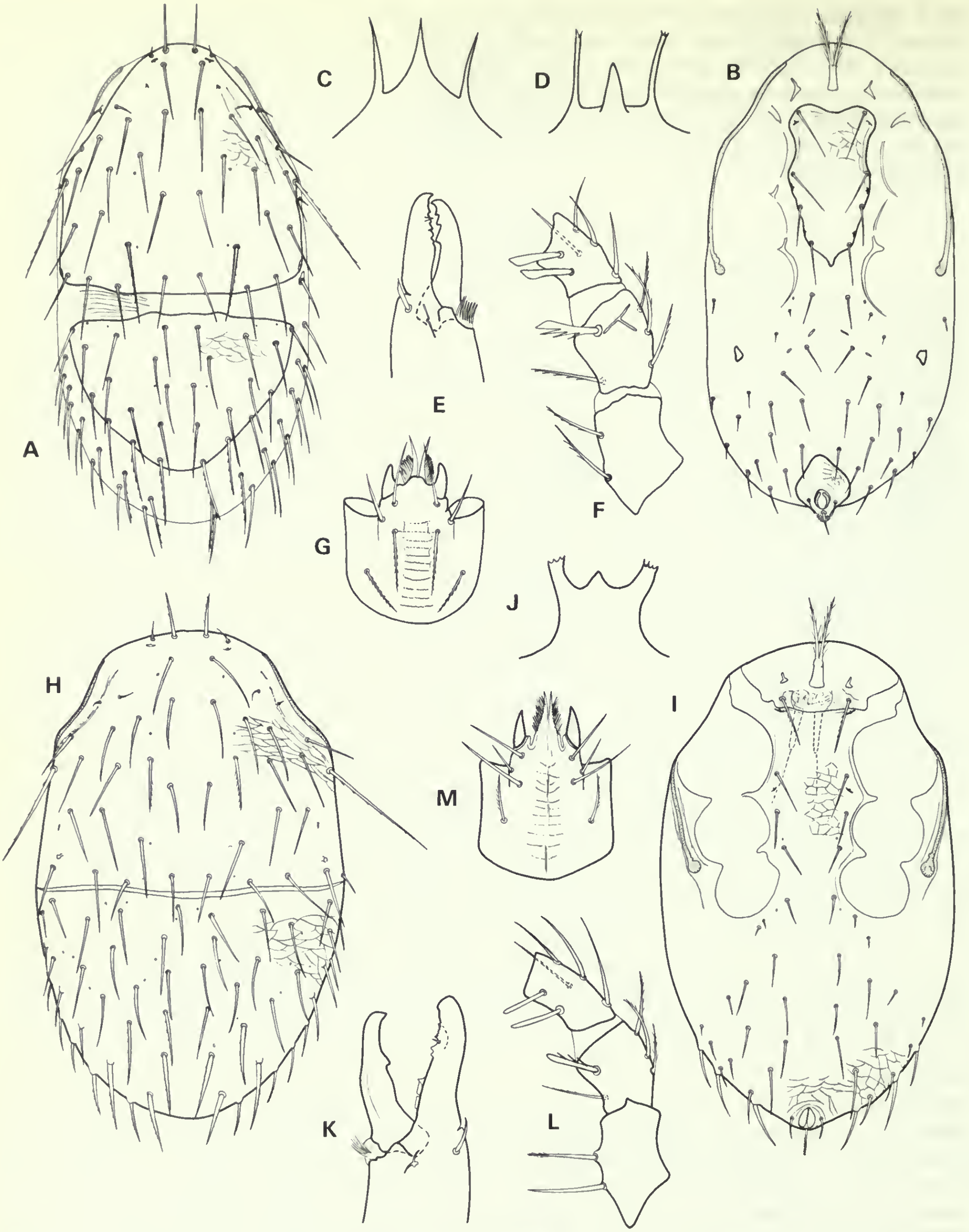

Fig. 26 *Vulgarogamasus kraepelini* (Berlese), **deutonymph** – A dorsum; B venter; C, D tectum; E chelicera; F palp trochanter, femur and genu; G venter of gnathosoma: **male** – H dorsum; I venter; J tectum; K chelicera; L palp trochanter, femur and genu; M venter of gnathosoma.

in figure 26K. The spermatophoral process is only apparent as an enlargement of the basal half of the movable digit. The fixed digit bears three small teeth and half a dozen very small denticles. The chaetotaxy of the palp trochanter, femur and genu is shown in figure 26L, and the venter of the gnathosoma in figure 26M. Leg I bears very fine setae. Leg II is as in figure 27A, the lower inner spur on the femur being sometimes pointed or irregular. Leg III bears stouter setae than leg I, whilst leg IV bears stouter setae again and on the tarsus an erect pilose seta *c.* 175 μm long.

FEMALE: The podonotal shield (396–504 μm long × 444–540 μm wide) is entirely reticulated and bears 22 pairs of setae which are generally of even length and individually pass the bases of the next. Only *r3* are longer and stout and pilose (Fig. 27B). The opisthonotal shield (360–456 μm long × 432–528 μm wide) is also entirely reticulated. It bears 25 pairs of setae of which a number of the more posterior pairs are clearly pilose distally.

The tritosternum has a narrow base and pilose laciniae, and the presternal shields are very small. Sternal setae I are situated anterior to the sclerotized part of the sternal shield which is itself generally deeply indented posteriorly (Fig. 27C). This indentation can be irregular or even sealed off from the posterior margin. The genital shield is broad and pointed anteriorly and has a pair of lateral horns. All the ventral setae are fine and slender. The postanal seta is stouter and longer than the paranals. The peritreme extends to coxa I.

The tectum is as in figure 27D, the only variation noted being that the centre prong may be considerably shorter. The chelicera is shown in figure 27E, the palp trochanter, femur and genu in figure 27F, and the venter of the gnathosoma in figure 27G. The setae of leg I are long and fine, leg II bears considerably stouter setae, whilst on leg III they are mainly slender. Leg IV bears predominately stout long setae, a number of which are erect and often finely pilose.

MATERIAL EXAMINED. 61 samples – 24 DNN, 17 ♂♂, 80 ♀♀.

ENGLAND: Gloucestershire, Hampshire, Essex, Berkshire, Buckinghamshire, Nottinghamshire, Cheshire, Lancashire, Cumberland, Northumberland.

WALES: Monmouthshire, Merionethshire.

SCOTLAND: Roxburghshire, Midlothian, Argyllshire, Aberdeenshire, Perthshire, Angus, Ross and Cromarty, Inner Hebrides (Mull, Ulva), Shetland.

IRELAND: Dublin, Kildare, Westmeath.

Thirty-three of the samples examined are from Scotland. Habitats are wide ranging, viz. on small mammals and in their nests, an ants' nest, coniferous and deciduous litter, mosses, grassland, flood debris, rotten wood and on fungi.

DISTRIBUTION: Previous British records are those of Halbert (1915) who recorded the male from decayed fungi at Glendalough, Co. Wicklow, and a female as *Gamasus (Eugamasus) magnus* Kramer, which I have examined, from amongst moss in Knappagh Wood, Westport, Co. Mayo, August 1911. Hull (1918) recorded it from Northumberland, Ireland (presumably Halbert's record), and the Isle of May, Scotland, and Curry (1969) collected it in grassland in Co. Kildare. Turk & Turk's (1952) record of a female of *Parasitus intermedius* (Berlese) from Delamere, Cheshire, 22 March 1925, is referrable to this species. Hull (1917) considers that *Parasitus vespillonum* Oudemans, 1902*b* is the deutonymph of *kraepelini,* but three deutonymphs of *vespillonum* (the only stage described) in the Oudemans Collection closely resemble small specimens of *Parasitus consanguineus* Oudemans & Voigts. As already pointed out by Micherdzinski (1969) the record of this species by Turk (1945) from Bagley Wood, Oxfordshire, is clearly an error of identification and the specimens are not available for comment.

This species is recorded from Iceland (Sellnick, 1940), Finland (Nordberg, 1936), Sweden (Trägårdh, 1910), Germany (Berlese, 1905, 1906, Schweizer, 1925, Willmann, 1939*b*, 1951*a*, Holzmann, 1969, Karg, 1965, 1971), Austria (Franz, 1943, Leitner, 1946, Willmann, 1951*b*), Switzerland (Schweizer, 1961), Czechoslovakia (Willmann, 1954, 1956, Mrciak & Rosicky, 1956, Halašková, 1959), Hungary (Willmann, 1938*a*), Poland (Pax & Maschke, 1935, Willmann, 1956, Micherdzinski, 1969) and the U.S.S.R. (Pinchuk, 1976) and Western Siberia (Davydova, 1969, 1976).

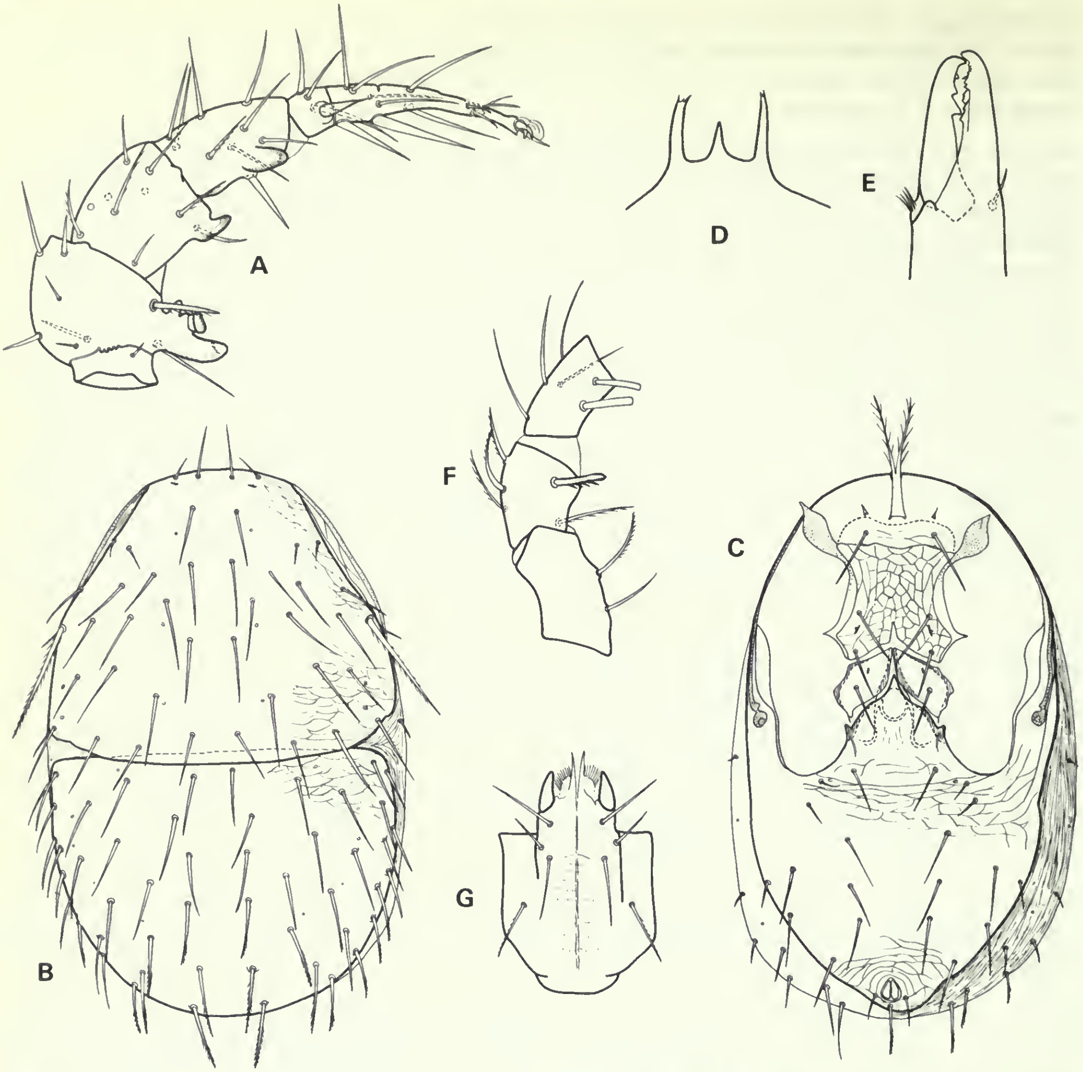

Fig. 27 *Vulgarogamasus kraepelini* (Berlese), **male** – A leg II: **female** – B dorsum; C venter; D tectum; E chelicera; F palp trochanter, femur and genu; G venter of gnathosoma.

Vulgarogamasus oudemansi (Berlese) comb. nov.
(Figs 28A–N; 29A–F)

Parasitus emarginatus (C. L. Koch, 1839) sensu Oudemans, 1902*b*: 40.
Gamasus (Eugamasus) oudemansi Berlese, 1904*b*: 280; 1906: 167.
Eugamasus oudemansi: Willmann, 1936*b*: 195. Athias-Henriot, 1979: 7.
Parasitus oudemansi: Micherdzinski, 1969: 563. Holzmann, 1969: 16. Karg, 1971: 448.
Parasitus (Eugamasus) oudemansi: Tichomirov, 1969: 1475. Bregetova *et al.*, 1977: 63, 69.

Bregetova (1956) followed Oudemans (1914) in suggesting that the male of *oudemansi* may be a heteromorphic form of *magnus* although Willmann (1936*b*) had found males and females of *oudemansi* together and had figured the female which is distinct from that of *magnus.* Holzmann (1969) and Bregetova *et al.* (1977) treat *oudemansi* as a distinct species. In the present study the incidence of males and females occurring together, plus the fact that one of the deutonymphs was showing the developing male within, and the combinations of chaetotactic and other external morphological differences which are apparent from the figures, leave no doubt that *oudemansi* is a distinct species.

DEUTONYMPH. The podonotal shield (470–490 μm long × 460–530 μm wide) is entirely reticulated and bears 20 pairs of setae, *s2* being off the shield (Fig. 28A). The shortest setae are *z1, s1, s2* and *r2* and the longest is *r3,* but the remainder are longer than average and most surpass the base of the next, with *z2* being slightly stouter. A number, especially *j1* and *r3*, are finely pilose to some degree. The opisthonotal shield (310–320 μm long × 420–455 μm wide) is also entirely reticulated and bears 13 pairs of longish setae similar to those of the podonotal shield. The setae on the posterior membrane arise from strong bases and are similar and may be slightly pilose at their tips.

The tritosternum has a narrow base and pilose laciniae. It is flanked by a pair of very small presternal shields (Fig. 28B). The sternal shield (310–320 μm long) is entirely reticulated and of a rather conspicuous symmetrical outline, the anterior margin being strongly undulated and reminiscent of some *Pergamasus* deutonymphs. The sternal setae are slightly longer than the opisthogastric setae and may show some pilosity. The reticulated anal shield is attenuated anteriorly, whilst the postanal seta is slightly longer than the paranals. The peritreme extends to coxa I.

The trispinate tectum may have the slender lateral prongs finely bifid at their tips (Fig. 28C). The chelicera is shown in figure 28D, and the venter of the gnathosoma in figure 28E. The palpcoxal setae are finely pilose. The palp trochanter, femur and genu are as in figure 28F. The leg setae are basically simple, although some show small degrees of pilosity. The femur and tarsus of leg IV each bear dorsally a long fine seta measuring *c.* 200 μm and *c.* 250 μm respectively.

MALE. The dorsum is strongly sclerotized, entirely reticulated, and divided medially by a transverse suture. It measures 980–1140 μm long × 564–650 μm wide (Fig. 28G). The podonotal region bears 23 pairs of setae: *z1, s1, s2* and *r4* are the shortest, *r3* is the longest (*c.* 265 μm) and is very finely but sparsely pilose. The remaining setae are slender and some show traces of pilosity. The opisthonotal region bears about 25–27 pairs of strong setae similar to the majority on the podonotum.

The tritosternum has a narrow base and pilose laciniae. It is flanked by a pair of conspicuous triangular presternal shields (Fig. 28H). The holoventral shield is heavily sclerotized except for the narrow area in front of sternal pores I. The genital lamina protrudes from the anterior edge of the sternal shield. Sternal setae IV–V are shorter than I–III, but the opisthogastric setae are longer again and some are finely pilose. The paranal setae are only slightly shorter than the postanal. The peritreme extends to coxa I.

The typical tectum comprises a broad triangular plate, somewhat uneven in outline, with a pair of lateral teeth set well back (Fig. 28I). In some of the specimens it is lacking at least one of the teeth and is more uneven (Fig. 28J). The chelicera is shown in detail in figure 28K: the cluster of fine teeth adjacent to the *pilus dentilis* show considerable variation in their contour, due partly to their formation and partly to the angle of view. The chaetotaxy of the palp trochanter, femur and genu is as in figure 28L. In one specimen examined the stout proximal seta of the trochanter is of normal thickness on the right palp, but only half as thick on the left, and the corniculi have rounded, not pointed, tips. The venter of the gnathosoma is shown in figure 28M. The internal posterior hypostomatic setae are the longest, the palpcoxal setae are finely pilose, and the corniculi are strong and bold. Leg II is shown in detail in figure 28N. Some of the setae are finely pilose. The majority of setae on leg I are fine and slender, but a single short stout dorsal seta is present on both the trochanter and the femur. Leg III bears generally stouter setae than leg I, whilst on leg IV they are also stouter and some are sinuous.

FEMALE. The podonotal shield (516–564 μm long ×526–600 μm wide) is completely reticulated and bears 21 pairs of setae (Fig. 29A), but in the specimen figured there is no trace of the right *z5* although its associated pore is present. Setae *z1, s1, s2* and *r2* are considerably

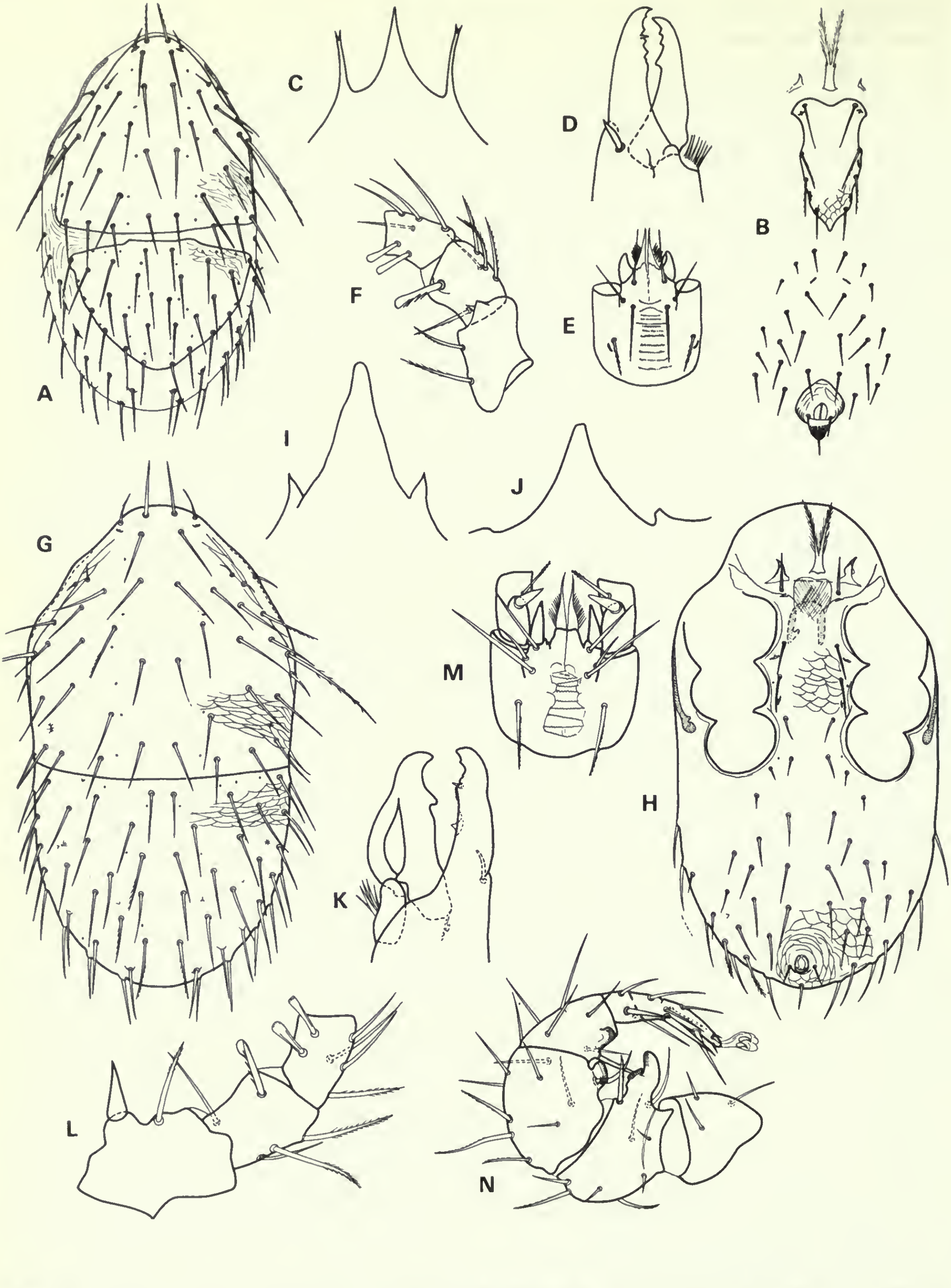

Fig. 28 *Vulgarogamasus oudemansi* (Berlese), **deutonymph** – A dorsum; B venter; C tectum; D chelicera; E venter of gnathosoma; F palp trochanter, femur and genu: **male** – G dorsum; H venter; I, J tectum; K chelicera; L. palp trochanter, femur and genu; M venter of gnathosoma and palp trochanters; N leg II.

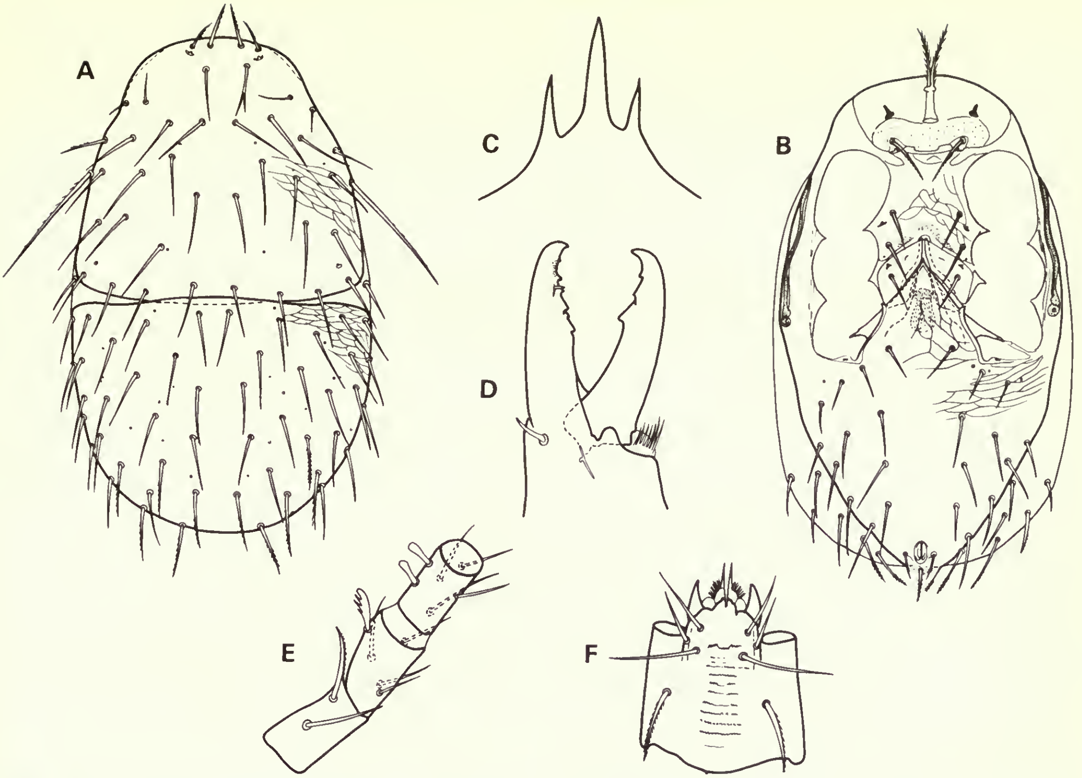

Fig. 29 *Vulgarogamasus oudemansi* (Berlese), **female** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma.

longer than in most other species; *s1* and *s2* are very fine; *r3* are *c.* 240 µm in length and bear sparse traces of pilosity. The opisthonotal shield (480–516 µm long × 540–660 µm wide) is also entirely reticulated and bears 24 pairs of symmetrically arranged setae. Most reach or surpass the bases of the next and a few are pilose to some extent.

The tritosternum has a narrow base and pilose laciniae. It is flanked by a pair of rather granular presternal shields (Fig. 29B). The sternal shield is granular and concave distally. The sternal setae are slightly stouter than the metasternals and genitals. The genital shield is triangular and has a small pair of lateral horns midway. The ten or eleven pairs of opisthogastric setae are strong and simple. The postanal seta is pilose and the paranals simple. The peritreme extends to coxa I.

The tectum comprises a stout central prong and a pair of shorter slightly divergent lateral prongs (Fig. 29C). The chelicerae have a fine granular region between the distal teeth of the fixed digit (Fig. 29D). The chaetotaxy of the palp trochanter, femur and genu is shown in figure 29E, and the venter of the gnathosoma in figure 29F. As in the male, the internal posterior hypostomatic setae are the longest, the palpcoxal setae are finely pilose, and the corniculi are strong and bold. The setae on leg I are fine and slender. Leg II bears ventrally two conspicuous stout setae on the trochanter, one on the femur, two on the genu, two on the tibia and three on the tarsus. Leg III bears stout ventral setae on the genu, tibia and tarsus. Leg IV bears stout setae on the femur, genu and tarsus, those on the tarsus being the longest.

MATERIAL EXAMINED. 19 samples – 3 DNN, 36 ♂♂, 37 ♀♀.
ENGLAND: Somerset, Hampshire, Surrey, Essex, Buckinghamshire, Bedfordshire, Cambridgeshire, Cheshire, Durham.
SCOTLAND: Midlothian, Roxburghshire, Perthshire, Isle of Rhum.
IRELAND: Cork.

Most specimens were collected from the nests of small mammals and birds, including three females from the nest of Manx shearwater *Procellaria puffinus* Brünnich on the Isle of Rhum, Inner Hebrides.

DISTRIBUTION. The only previous record for the British Isles is that of Hull (1918) who recorded it from moles' nests in Northumberland.

It is recorded from Iceland (Sellnick, 1940), Sweden (Lundqvist, 1974), Holland (Oudemans, 1902*b*, 1912*a*, 1914) Germany (Oudemans, 1903*a*, Holzmann, 1969, Karg, 1971), Austria (Franz, 1943, Willmann, 1951*a*), Poland (Kielczewski, 1957, Zukowski, 1958), Czechoslovakia (Willmann, 1936*b*, Maschke, 1936) and Western Siberia (Davydova, 1969, 1976).

Vulgarogamasus remberti (Oudemans)
(Figs 30A–G; 31A–L)

Eugamasus remberti Oudemans, 1912*b*: 243; 1912*d*: Verslag LI; 1914: 131. Holzmann, 1969: 17.
Parasitus remberti: Micherdzinski, 1969: 588. Karg, 1971: 447.
Parasitus (Vulgarogamasus) remberti: Tichomirov, 1969: 1336, 1476. Bregetova *et al.*, 1977: 81, 83.

DEUTONYMPH. The podonotal shield (277–300 μm long × 300–324 μm wide) is reticulated and bears 20 pairs of fine slender setae (Fig. 30A), of which *s2* are situated off the shield and *r3* are the longest (*c.* 125 μm). Setae *z5* are only slightly longer than adjacent setae. The opisthonotal shield (228–252 μm long × 276–312 μm wide) is also reticulated. It bears 14 pairs of slender simple setae of almost equal length and the surrounding posterior membrane bears similar setae.

The tritosternum has a narrow base and pilose laciniae. It is flanked by a pair of lightly sclerotized presternal shields (Fig. 30B). The sternal shield (*c.* 215 μm long) is reticulated, the setae are slender and simple, as are the fifteen or so pairs of opisthogastric setae. The reticulated anal shield is widened anteriorly and invariably bears one pair of preanal setae at

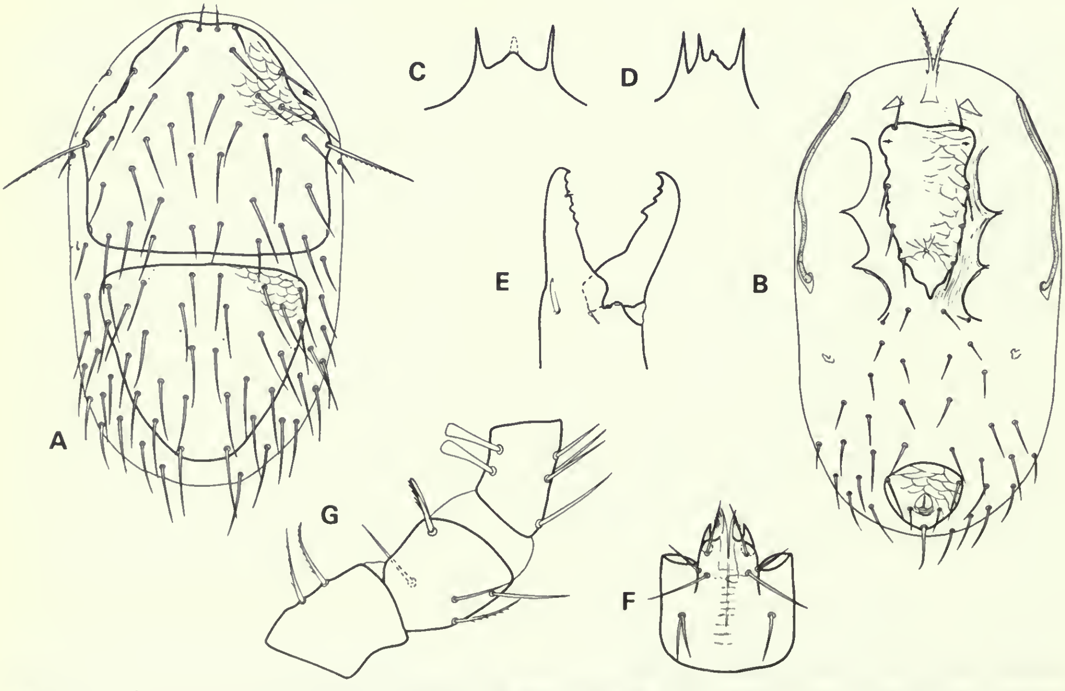

Fig. 30 *Vulgarogamasus remberti* (Oudemans), **deutonymph** – A dorsum; B venter; C, D tectum; E chelicera; F venter of gnathosoma; G palp trochanter, femur and genu.

its outermost anterior angles. The paranal setae are approximately half the length of the stouter postanal seta. The peritreme extends to coxa I.

The tectum is essentially trispinate (Fig. 30C), but irregularities occur (Fig. 30D). The movable digit of the chelicera bears three well-defined teeth, but on the fixed digit the teeth are small and less regular (Fig. 30E). The venter of the gnathosoma is shown in figure 30F: the internal posterior hypostomatic setae are the longest and, in the specimen figured, one of the palpcoxal setae is forked from its base. The corniculi are small. The palp trochanter, femur and genu are shown in figure 30G. The leg setae are simple and mainly fine and slender, whilst on leg IV, and in particular on the tarsus, several larger curved setae are present.

MALE. The dorsum (468–528 μm long × 216–276 μm wide) is entirely reticulated and is divided medially by a transverse suture (Fig. 31A). The podonotal region bears 23 pairs of simple slender setae of which *r5* are the longest (*c.* 80 μm), *s2* are very short, and *r4* are clearly visible behind *r3*. The opisthonotal region bears about 30 pairs of similar setae arranged symmetrically.

The tritosternum has a short narrow base and pilose laciniae. The presternal shields are small and barely discernible (Fig. 31B). The holoventral shield is reticulated but generally weakly sclerotized. All the setae are simple. The genital aperture protrudes anterior to sternal setae I. The postanal seta is more than twice the length of the paranals. The peritreme extends to coxa I.

The tectum comprises three prongs, the central one may be rudimentary and irregular, but the laterals are always well developed (Fig. 31C). The chelicera is shown in detail in figure 31D. The movable digit (*c.* 45 μm) bears a single tooth and the fixed digit, which is slightly clubbed distally, a row of up to six very small teeth. The chaetotaxy of the palp trochanter, femur and genu is shown in figure 31E, and the venter of the gnathosoma in figure 31F. The corniculi are small. Leg II is shown in detail in figure 31G: no variation in the formation of the spurs has been noted. The setae on leg I are fine and slender and those on legs III and IV somewhat stouter and longer.

FEMALE. The podonotal shield (*c.* 300 μm long × 380 μm wide when flattened) is rather weakly sclerotized and only partly reticulated (Fig. 31H). It bears 21 pairs of setae of which *s2* may be on or off the shield. Setae *r3* are the longest (*c.* 105 µm) and *z5* are slightly longer and stouter than adjacent setae. The opisthonotal shield (*c.* 330 μm long × 380 μm wide when flattened) is also weakly sclerotized and bears 25 or more pairs of simple setae in the specimen figured. In other specimens this shield appears not to extend ventrally, so consequently the number of setae on the sclerotized area is reduced. These specimens differ also from the figured specimen in that the opisthonotal setae are considerably shorter, shorter in fact than those figured by Holzmann (1969), and podonotal setae *j4* and *z5* are slightly stouter than those adjacent to them, a feature not shown by Holzmann, but shown by Oudemans (1914). I can, however, see no differences in the ventral sclerotization and chaetotaxy of these specimens or in the other features described and figured. Clearly more material needs to be examined.

The tritosternum has a narrow base and pilose laciniae, but there is only the slightest trace of presternal shields (Fig. 31I). Anteriorly the sternal shield is weakly sclerotized, but it becomes more clearly defined posteriorly from sternal setae II. All ventral setae are strong and simple. The genital shield is almost triangular in its anterior two thirds and it terminates in a narrow tip. The opisthogastric shield is undulating in outline but is fairly symmetrical. The postanal seta is of similar stoutness to the ventral setae, but the paranals are thinner and a little shorter. The peritreme extends to coxa I.

The tectum (Fig. 31J) is basically as in the male and deutonymph, with similar variation in the centre prong. The chelicera is shown in figure 31K. The chaetotaxy of the pedipalp is as in the male (Fig. 31E), and the venter of the gnathosoma is shown in figure 31L. The leg setae are basically simple and are most slender on leg I.

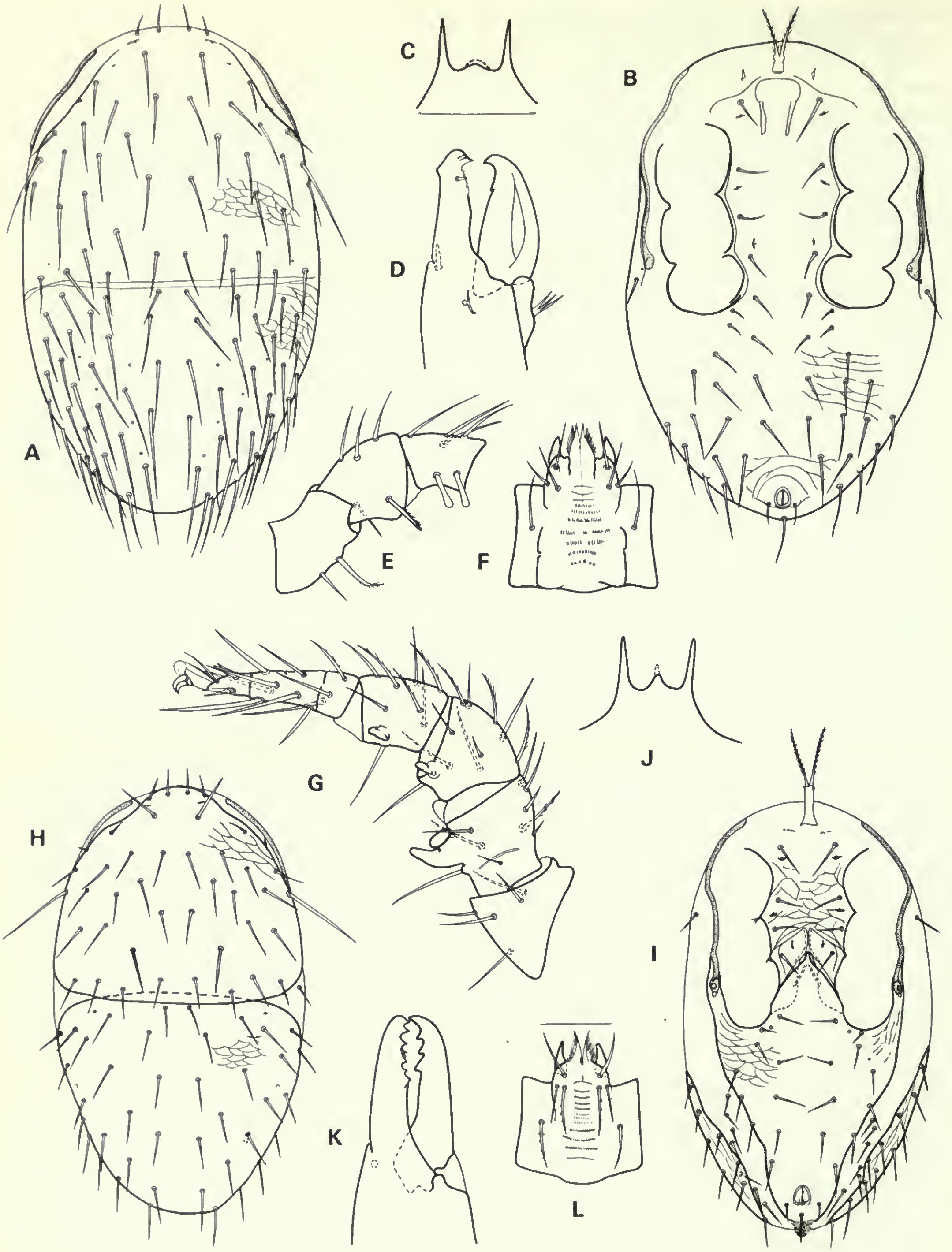

Fig. 31 *Vulgarogamasus remberti* (Oudemans), **male** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma; G leg II: **female** – H dorsum; I venter; J tectum; K chelicera; L venter of gnathosoma.

MATERIAL EXAMINED. 13 samples – 1 PN, 29 DNN, 9 ♂♂, 6 ♀♀.
ENGLAND: Gloucestershire, Wiltshire, London, Cambridgeshire.
SCOTLAND: Roxburghshire, Midlothian, West Lothian, Angus, Argyllshire (Lismore), Inverness-shire (Rhum).

Most specimens were collected from nests of the mole *Talpa europaea* L., but others are from *Sorex, Apodemus* and *Microtus,* and also the drey of grey squirrel *Sciurus carolinensis* Gmelin and old nests of blackbird *Turdus merula* L., tawny owl *Strix aluco* L. and Manx shearwater *Procellaria puffinus* Brünnich.

DISTRIBUTION. The only previous British record of this species is that of Mead-Briggs and Hughes (1966) who examined specimens from rabbits *Oryctolagus cuniculus* (L.) in Fifeshire.

It is recorded from Iceland (Sellnick, 1940), Sweden (Lundqvist, 1974), Finland (Nordberg, 1936), Holland (Oudemans, 1912*d,* 1914), Belgium (van Daele & Heungens, 1974), Germany (Willmann, 1938*b*, 1952*b*, Karg, 1965, 1971, Holzmann, 1969), Austria (Willmann, 1951*b*), Czechoslovakia (Willmann, 1952), Poland (Willmann, 1952*b*), the U.S.S.R. (Pirjanik, 1962, Bregetova, 1956, Pinchuk, 1976) and Western Siberia (Davydova, 1969, 1976). Most records are of specimens associated with small mammals, especially mice and voles.

Vulgarogamasus trouessarti (Berlese)

(Figs 32A–N; 33A–F)

Gamasus thalassinus Berlese & Trouessart, 1889; [121–143] (not seen), non Grube, 1861, teste Berlese, 1892*a*: 67.
Gamasus Trouessarti Berlese, 1892*a*: 67 (non 1902 auctt. including Micherdzinski, 1969 and Karg, 1971).
Gamasus (Eugamasus) Trouessarti: Berlese, 1906: 182.
Eugamasus trouessarti: Holzmann, 1969: 16.
Parasitus trouessarti: Micherdzinski, 1969: 512. Karg, 1971: 447.
Parasitus (Vulgarogamasus) trouessarti: Tichomirov, 1969: 1336, 1476. Bregetova *et al.,* 1977: 80, 81.
Gamasus (Eugamasus) excurrens Berlese, 1904*b*: 263; 1906: 165, 166.

DEUTONYMPH. The two deutonymphs examined are both weakly sclerotized. The podonotal shield (520–540 μm long × 510–530 μm wide) is reticulated and bears 22 pairs of simple setae, *r5* are the longest, the remainder of almost equal length (Fig. 32A). Setae *j1* are unusually well separated and *s2* and *r2* are off the shield. The reticulated opisthonotal shield is small (380–390 μm long × 370–390 μm wide) and bears 14 pairs of setae of approximately equal length, the setae on the posterior membrane are similar.

The tritosternum has a narrow base and pilose laciniae. The presternal shields are weakly sclerotized. The sternal shield (Fig. 32B) is 395–405 μm long and is lightly reticulated. The sternal and opisthogastric setae are simple. The anal shield bears four preanal setae on one specimen (Fig. 32B) and five on the other (Fig. 32C). The paranal setae are fine, the postanal longer and stout. The peritreme is slender and does not reach coxa I.

The tectum is multidenticulate with a median and two lateral cusps (Fig. 32D). The chelicera is shown in figure 32E, and the chaetotaxy of the palp trochanter, femur and genu in figure 32F. The gnathosomal setae are simple and the corniculi are strong (Fig. 32G). The majority of the leg setae are quite fine and slender, but stout sinuous setae are present mainly on legs III and IV.

MALE. The idiosoma is entirely sclerotized and reticulated, but dorsally the podonotal and opisthonotal regions are separated by a broad unsclerotized strip which extends the whole width of the idiosoma (Fig. 32H). The podonotal region (552–580 μm long × 540–552 μm wide) bears 25 pairs of setae of which a few appear to be finely pilose on one margin at least. The verticals, *j1,* are well separated, *r3* are the longest (*c.* 160 μm), and the remainder are all roughly equal in length (*c.* 100 μm). The opisthonotal region (480–504 μm long × 504 μm wide) bears about 31 pairs of symmetrically arranged setae of even length.

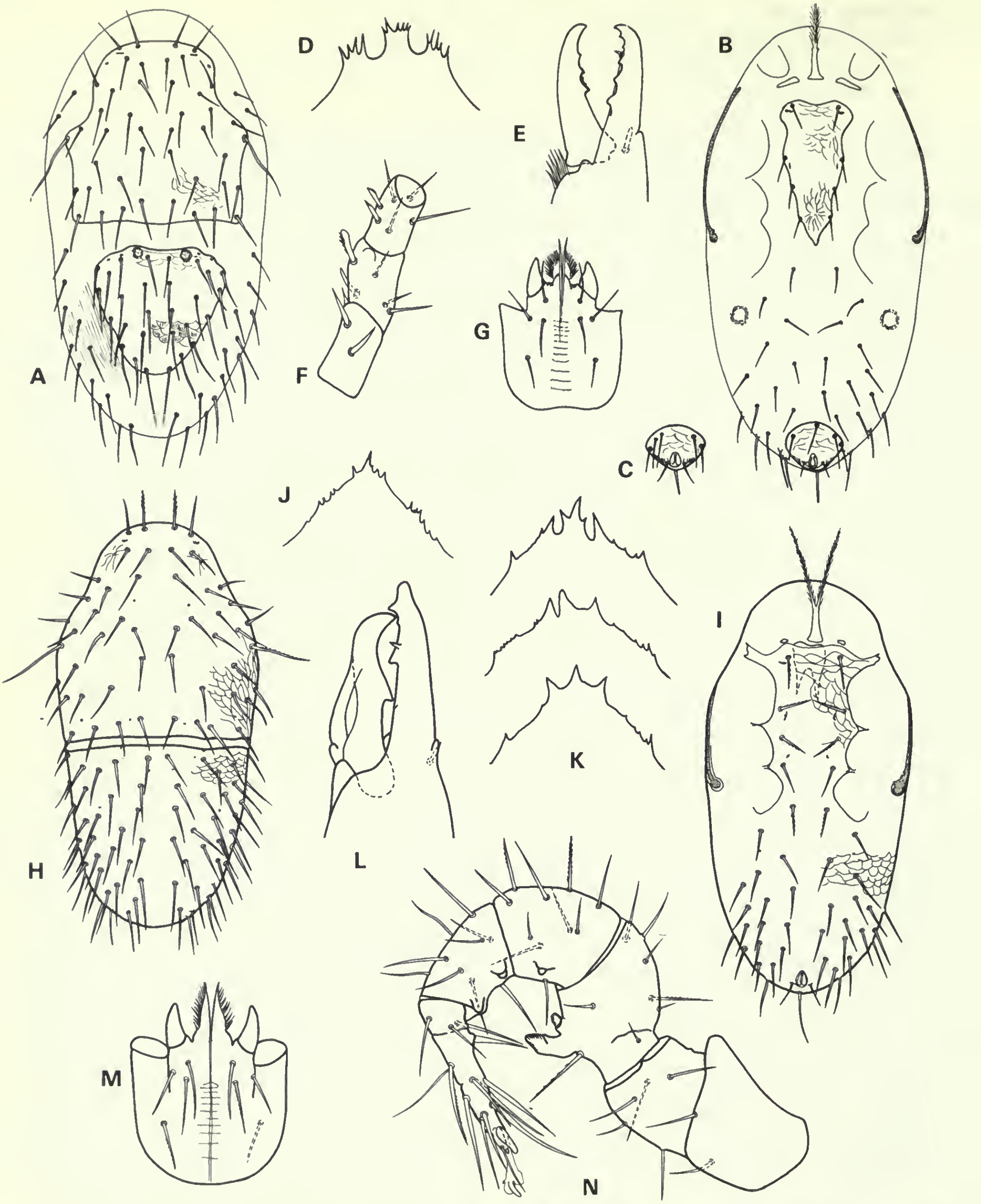

Fig. 32 *Vulgarogamasus trouessarti* (Berlese), **deutonymph** – A dorsum; B venter; C anal shield; D tectum; E chelicera; F palp trochanter, femur and genu; G venter of gnathosoma: **male** – H dorsum; I venter; J, K tectum, showing variation; L chelicera; M venter of gnathosoma; N leg II.

The tritosternum has a narrow base and long pilose laciniae. The presternal shields are small or even lacking (Fig. 32I). The venter is well sclerotized and reticulated. Some of the

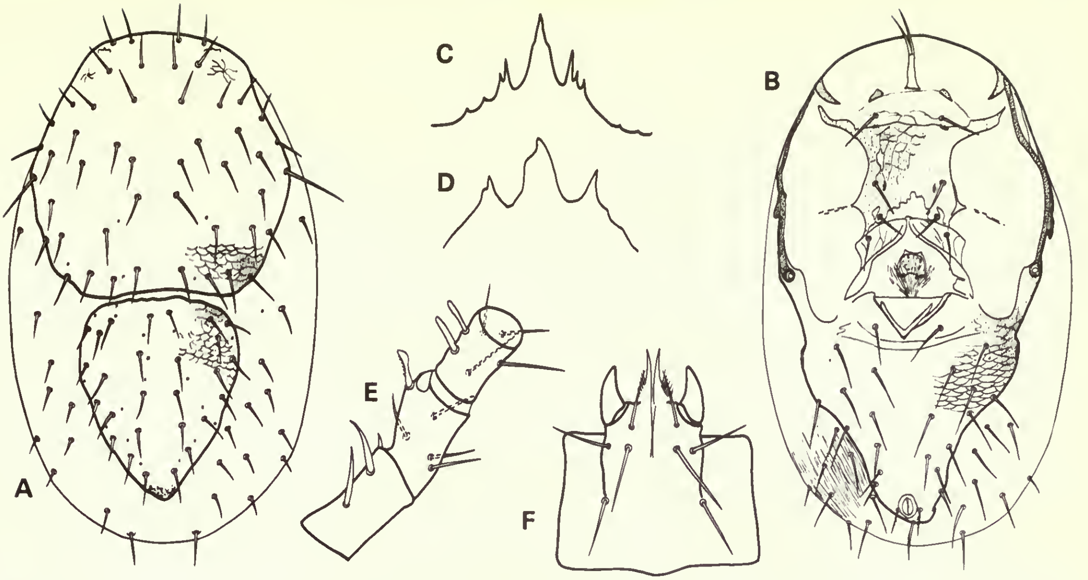

Fig. 33 *Vulgarogamasus trouessarti* (Berlese), **female** – A dorsum; B venter; C, D tectum, showing variation; E palp trochanter, femur and genu; F venter of gnathosoma.

ventral setae show traces of pilosity. The paranal setae are fine, the postanal stouter and twice as long. The peritreme extends just to coxa I.

The tectum comprises an irregularly toothed prominence. A fairly symmetrical example is shown in figure 32J, whilst variations from three specimens collected together are shown in figure 32K. The chelicera is shown in figure 32L. The chaetotaxy of the pedipalp is as in the female (Fig. 33E), and in both sexes a broad conical spur on the femur lies adjacent to the anterolateral seta. The venter of the gnathosoma is shown in figure 32M: the corniculi are stout and in the specimen figured, there is no trace of one of the palpcoxal setae. Leg II is shown in detail in figure 32N. The distal protuberance on the tibia is inconspicuous, but is shown in heavy outline for emphasis. The majority of the setae on the other legs are fine and simple, but on leg IV longer and stouter setae are apparent.

Female. The dorsal shields are well sclerotized, reticulated, granular and are of conspicuous outline (Fig. 33A). The podonotal tapers from its midpoint and the opisthonotal, which is pear shaped, continues the effect of this taper. The podonotal shield (600–630 μm long × 528–570 μm wide) bears 24 pairs of setae. The verticals, *j1*, are well separated as in the deutonymph. Setae *r3* are the longest (*c.* 105 μm), but others approach this length. The opisthonotal shield (423–460 μm long × 360–408 μm wide) bears generally 14 pairs of setae, but in the specimen figured one seta is missing from the right side, whilst in others 15 setae are present on one side, or they may be evenly paired.

The tritosternum has a narrow base and pilose laciniae. The presternal shields are triangular and granular (Fig. 33B). Basically the ventral shields are all granular and well sclerotized, but the sternal is weak and transparent anterior to pore I and also along its irregular posterior margin. The genital shield is broad and triangular, but in the specimen figured it is folded back. The opisthogastric shield is frequently of asymmetrical outline. The anal setae are partly pilose and are slender, the postanal being the longest. All other ventral setae are slender and simple. The peritreme extends just to coxa I.

A well-formed tectum is shown in figure 33C. It has the central portion in the form of a single broad tooth and the two flanking cusps are toothed, but not as prominently as in the deutonymph, whilst further back are short spines variously developed. A less regularly formed specimen is shown in figure 33D. The chelicerae are as in the deutonymph (Fig. 32E). The chaetotaxy of the pedipalp is shown in figure 33E: the femur bears a distal broad conical tooth adjacent to the anterolateral seta. The venter of the gnathosoma is shown in figure 33F: the corniculi are strong. Leg I bears very fine setae, and on legs II–IV the setae become progressively stouter whilst retaining their fineness.

MATERIAL EXAMINED. 7 samples – 2 DNN, 10 ♂♂, 10 ♀♀.
ENGLAND: Devon, Hampshire, Durham.
WALES: Anglesey.
SCOTLAND: Aberdeenshire.

This exclusively seashore species is, despite the scarcity of records, probably found throughout the British Isles, but its frequency parallels that of *Vulgarogamasus immanis* (p. 292) and not *Parasitus kempersi* (p. 280). Halbert (1915, 1920), however, considered *trouessarti* to be abundant.

DISTRIBUTION. Previous British records are from Co. Mayo and Co. Dublin (Halbert, 1915, 1920), Northumberland and Lancashire (Hull, 1918), and Devon (Evans & Browning, 1954).

It is recorded from France and Norway (Berlese, 1904*b*, 1906) and Germany (Willmann, 1952*a*, Holzmann, 1969, Karg, 1971).

Genus ***EUGAMASUS*** Berlese

Eugamasus Berlese, 1892. *Acari, Myriopoda et Scorpiones hucusque in Italia reperta. Ordo Mesostigmata (Gamasidae).* Padova: 62.

TYPE SPECIES. *Gamasus magnus* Kramer, 1876.

Dorsal shield of male entire, with transverse suture; female and deutonymph with separate podonotal and opisthonotal shields. Setae of dorsal hexagon similar, varying only in length. Tritosternum normal, biramous, that of male not closely associated with genital orifice. Junction between sternal and metasternal shields of female oblique. Genital shield of female triangular or subtriangular. Opisthogaster with not more than 30 pairs of setae. Seta *al* of palp femur strongly multifid; setae al_1 and al_2 of palp genu bifid. Male chelicerae symmetrical. Corniculi short, entire. With the possible exception of coxa I, legs of deutonymph and female without spurs; only leg II of male spurred. Lobes of pulvilli rounded, normal.

Eugamasus magnus (Kramer)
(Fig. 34A–I)

Gamasus magnus Kramer, 1876: 91. Berlese, 1884, Fasc. 13: Nos 5, 6. Non Berlese, 1906: 177 = *E. berlesei* Willmann, 1935.
Parasitus magnus: Micherdzinski, 1969: 497. Karg, 1971: 449 (♂ only).
Parasitus (Eugamasus) magnus: Tichomirov, 1969: 1475. Bregetova *et al.*, 1977: 67, 71.
Eugamasus magnus: Holzmann, 1969: 15 (♂ only). Athias-Henriot, 1979: 5. Evans & Till, 1979: 209.
Eugamasus spinosustarsis Schweizer, 1961: 23. **Syn. nov.** Type examined.
Parasitus spinosustarsis: Micherdzinski, 1969: 503.

I have examined Schweizer's (1961) material of *spinosustarsis* and consider that the males are synonymous with *Parasitus magnus* (Kramer) as figured by Berlese (1884) and Micherdzinski (1969). Schweizer's single deutonymph is *P. coleoptratorum* and not *niveus* (= *loricatus*) as suggested by Micherdzinski (1969).

I am not prepared at present to state that *magnus* is in fact a distinct species from *berlesei.* Micherdzinski's treatment does not appear conclusive, whilst Holzmann's (1969) and Karg's (1971) keys to females leave one in doubt. One especially rich sample from a mole *Talpa europaea* L. nest examined in the present study contained seven species of Parasitinae including one male, twenty females and one deutonymph of *berlesei* and a single male of *magnus,* whilst, with one exception, the remaining samples from which male *magnus* were removed contained no *berlesei.* The exception is a slide already in the Museum collection (in cave, Sidcot Swallet, Somerset, July 1938) on which is mounted a typical male *magnus*

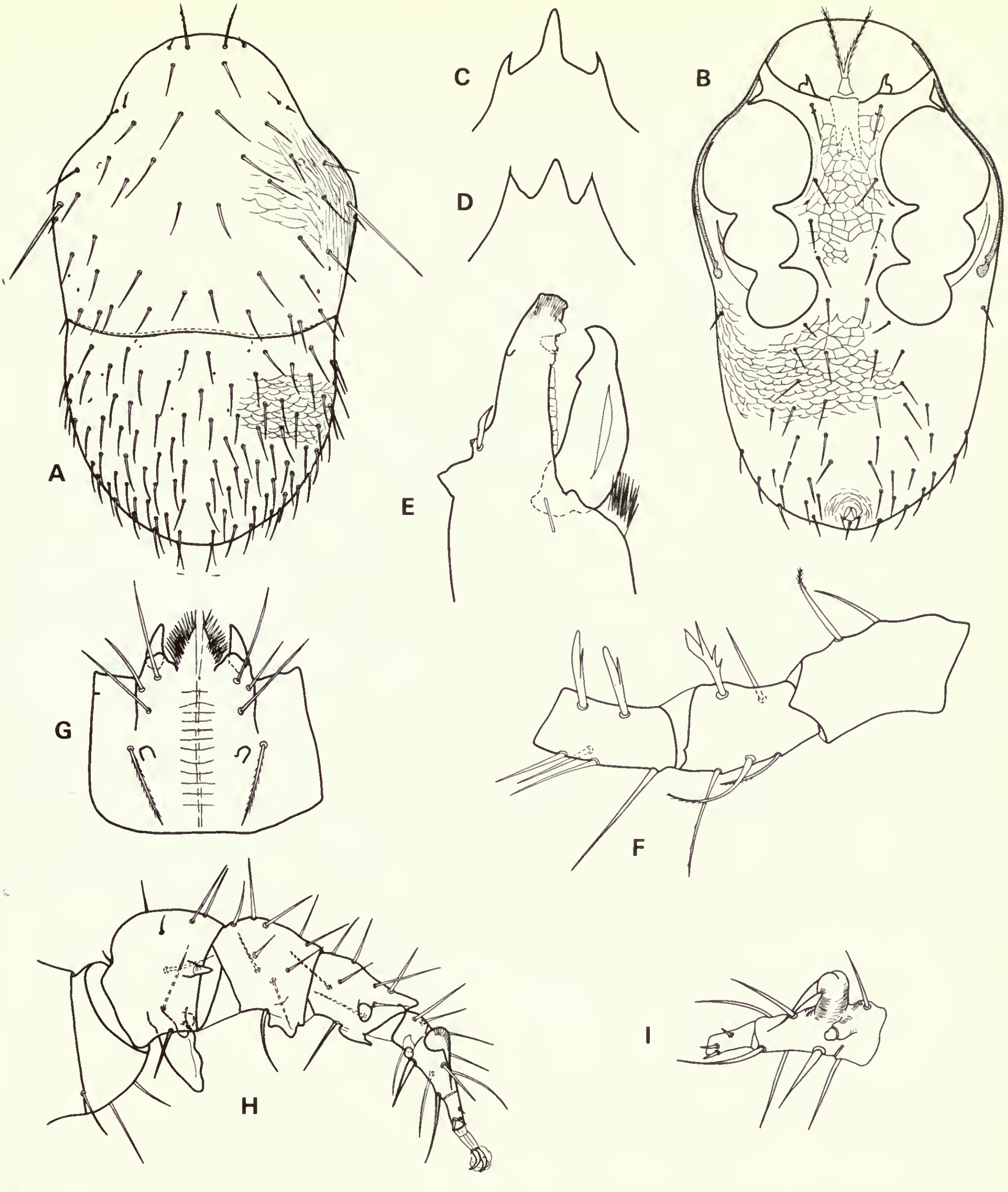

Fig. 34 *Eugamasus magnus* (Kramer), **male** – A dorsum; B venter; C tectum (typical); D tectum (irregular); E chelicera; F palp trochanter, femur and genu; G venter of gnathosoma; H leg II; I tarsus of leg II excluding the ambulacrum.

(1580 μm long) and a typical female *berlesei* (1280 μm long), presumably the only specimens collected.

Excluding a single specimen from Rydal Water, Westmorland, the males referred to here as *magnus* are considerably larger than those of *berlesei* and are readily distinguished on the armature of leg II.

DEUTONYMPH. Not examined.

MALE. The dorsum (1356–1620 μm long × 840–876 μm wide) is completely sclerotized and generally reticulated, although in the podonotal region the reticulations are less marked. A transverse suture extends across the centre of the dorsum (Fig. 34A). The podonotal region bears 24 pairs of setae of which only *r3* are long. The remainder are fine and simple, although *j1* show traces of pilosity. The opisthonotal region bears approximately 45–50 pairs of simple setae which are arranged for the most part symmetrically.

The tritosternum has a short base and long pilose laciniae. It is flanked by a pair of characteristically shaped presternal shields. The rest of the ventral surface is strongly sclerotized and evenly reticulated (Fig. 34B). All the setae are fine and slender. The genital lamina is not markedly prominent. The peritreme extends to the level of coxa I. The anus is small and the postanal seta is longer than the paranals.

The tectum is typically a broad central prong, rounded at its tip and flanked by a pair of inwardly directed short pointed prongs (Fig. 34C). In one specimen, described below, the tectum is as in figure 34D. The chelicera, shown in figure 34E, is heavily sclerotized. The movable digit is 150 μm long, rounded distally and bears one large tooth. The fixed digit is broad at its base with a large tooth-like protuberance and distal to this, a smaller one on the side of which is situated the dorsal seta. The inner edge of the digit bears a strip of fragmented membrane followed by a denticulate ridge adjacent to the *pilus dentilis,* a deep depression and an irregular large tooth. The tip of the fixed digit is broad. The chaetotaxy of the palp trochanter, femur and genu is shown in figure 34F. The venter of the gnathosoma is as in figure 34G. The palpcoxal setae are finely pilose and inwards from their bases arises a pair of small rounded protuberances. Coxa I bears a small but pronounced apical tooth dorsally. Leg II is shown in figure 34H, the most conspicuous feature being the strong apically directed spine on the dorsal margin of the tarsus (Fig. 34I). Leg I (*c.* 1860 μm) has all setae fine and slender, leg III (*c.* 1150 μm) bears ventrally on the genu two stout setae and on the tibia one, the remaining setae being simple, and leg IV (*c.* 1750 μm) has no exceptionally stout setae, but there is a small dorsal protuberance on the trochanter.

A single male from lakeside debris, Rydal Water, Westmorland, 29 November 1954, M. E. Bacchus coll., has the idiosoma 1100 μm long. The chaetotaxy is typical, but differs from the above description as follows: the tectum is as in figure 34D; the venter of the gnathosoma lacks the small protuberances; both legs II lack the small conical spur on the femur whilst the spur on the genu is considerably longer, one tibia has only one protuberance whilst the other has two, and one tarsus has the typical angular and pointed dorsal spur, but also a broad deep excrescence on the opposite side whereas the other tarsus has, in an almost ventral position, an angular spur with the point missing, but on the dorsal surface is a large conical spur. This specimen is clearly aberrant and although its size would place it in *berlesei*, the armature of leg II is predominantly *magnus.*

FEMALE. Not examined.

MATERIAL EXAMINED. 8 samples – 9 ♂♂.

ENGLAND: In Read's Cavern, Burrington, Somerset, 15 May 1940; in cave, Sidcot Swallet, Somerset, July 1938; in leaf litter (mainly oak), Robinswood Hill, Gloucester, 13 September 1959; in leaf litter, Earlswood, Warwickshire, 15 May 1962; in Hopping Piper Mine, Matlock Bath, Derbyshire, 18 May 1958; debris from middle zone, Rydal Water, Westmorland, 29 November 1954; in Ingleborough Cave, Clapham, Yorkshire, 21 November 1976.

SCOTLAND: In mole's nest, Midlothian/Roxburghshire borders, 1964.

DISTRIBUTION. Previous British records of *Eugamasus magnus* are most probably referrable to *E. berlesei* Willmann (*q. v.*). It has not been possible to examine with certainty any of the material of Hull (1918) which was identified as *magnus.* Halbert's (1915) record from Knappagh Wood, Westport, Co. Mayo is referrable to *Vulgarogamasus kraepelini* (*q. v.*). A single specimen (on a slide), from a dead bank-vole *Clethrionomys glareolus* (Schreber) from

Bagley Wood, Berkshire, identified by Vitzthum as *Eugamasus magnus* Kramer (Elton *et al.*, 1931), is a female deutonymph of *Parasitus loricatus,* therefore it is probably safe to say that *Eugamasus magnus* (Kramer) is now authentically recorded from the British Isles for the first time.

Eugamasus magnus is recorded (largely *teste* Micherdzinski, 1969) from Holland (Oudemans, 1914, 1913*c,* 1916), Belgium (Willmann, 1935, Leruth, 1939, van Daele & Heungens, 1974, 1975), France (Leruth, 1939), Germany (Kramer, 1876, Willmann, 1937, Holzmann, 1969, Karg, 1971), Austria (Leitner, 1946, Willmann, 1951*b*), Poland (Sellnick, 1940: 45, Kozlovski, 1955, Kielczewski, 1957, Micherdzinski, 1969), Hungary (Willmann, 1954), Czechoslovakia (Willmann, 1954, Mrciak & Rosický, 1956), Switzerland (Cooreman, 1959, Schweizer, 1961), Italy (Berlese, 1884), Jugoslavia (Willmann, 1941) and Finland (Willmann, 1938*c*). Davydova (1969) records *magnus* from Western Siberia but it is not clear whether *magnus* or *berlesei* are involved. In her second paper Davydova (1976) clearly figures both *magnus* and *berlesei,* again from Western Siberia.

Eugamasus berlesei Willmann
(Figs 35A–M; 36A–H)

Eugamasus magnus forma *berlesei* Willmann, 1935: 6.
Parasitus berlesei: Micherdzinski, 1969: 504. Karg, 1971: 449.
Parasitus (Eugamasus) berlesei: Bregetova *et al.*, 1977: 67, 71.
Eugamasus berlesei: Athias-Henriot, 1979: 7.
Gamasus (Eugamasus) magnus Kramer sensu Berlese, 1906: 177. Halbert, 1915: 50.
Eugamasus magnus (Kramer) sensu Schweizer, 1961: 22, and auctt.
Eugamasus magnus var. *monticola* Berlese sensu Schweizer, 1961: 26 (♀).
Gamasus magnus Kramer sensu Hull, 1918: 84.
Eugamasus anglocavernarum Turk, 1944: 150. Micherdzinski, 1969: 504. Type examined.

See also comments under *E. magnus,* p. 310.

DEUTONYMPH. The podonotal shield (456–580 μm long × 430–580 μm wide) is finely reticulated and bears 21–22 pairs of setae, *s2* being off the shield (Fig. 35A). The posterior margin of the shield in the specimen figured has five setae on the right and four on the left. Only setae *j1* and *r3* show fine traces of pilosity. Seta *z5* is only slightly longer than adjacent setae, *r3* is the only pair that is conspicuously long. The opisthonotal shield (340–380 μm long × 420–456 μm wide) is also finely reticulated. It bears 22 pairs of simple homogeneous setae, but in the specimen figured an extra unpaired seta is located posterior to *J1.* The interscutal membrane bears similar simple setae.

The tritosternum has a narrow base and pilose laciniae. The presternal shields are small. The reticulated sternal shield (324–370 μm long) is acuminate posteriorly and the setae slender and simple (Fig. 35B). The broadly oval anal shield is reticulated and bears an extra pair of setae (or even a third seta) anterolaterally (Fig. 35C). The opisthogastric setae (*c.* 20 pairs) are fine and simple. Irregularly shaped granular metapodal shields are present. The peritreme extends to coxa I.

The tectum comprises three strong tapered prongs, the laterals being occasionally bifid (Fig. 35D). The chelicera is shown in figure 35E. The chaetotaxy of the palp trochanter, femur and genu is as in figure 35F. The venter of the gnathosoma is shown in figure 35G: the corniculi are strong and pointed, the palpcoxal setae finely pilose, the other three pairs simple. The setae of leg I are simple; leg II bears stouter setae ventrally and on the tarsus; leg III has similar setae and the tarsus is swollen distally; leg IV has rather more stout setae.

MALE The idiosoma measures 1164–1350 μm long × 600–750 μm wide. It is heavily sclerotized and in many specimens is constricted in the region of the transverse suture (Fig. 35H). With the possible exception of *j1,* all setae are simple, slender and finely pointed. The dorsal chaetotaxy is shown in the figure; the podonotal region bears 24 pairs of setae of which only *r3* are long. The setae of the opisthonotal region, which number approximately 45–50 pairs, are occasionally asymmetrically arranged.

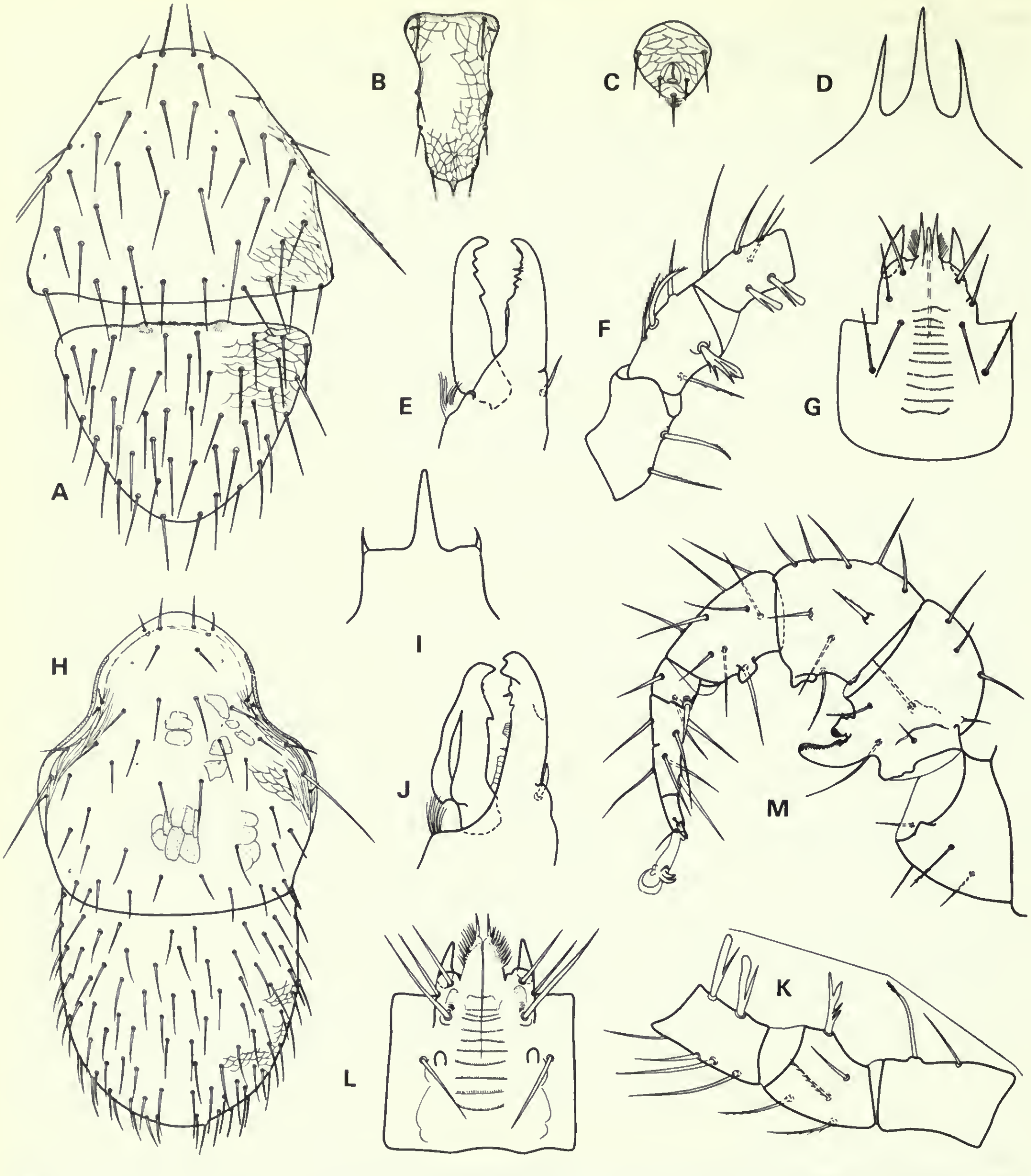

Fig. 35 *Eugamasus berlesei* Willmann, **deutonymph** – A dorsal shields; B sternal shield; C anal shield; D tectum; E chelicera; F palp trochanter, femur and genu; G venter of gnathosoma: **male** – H dorsum; I tectum; J chelicera; K palp trochanter, femur and genu; L venter of gnathosoma; M leg II.

The tritosternum has a narrow base and pilose laciniae and is flanked by characteristically shaped presternal shields. The ventral sclerotization and chaetotaxy appear identical to those of *E. magnus* (Fig. 34B).

The tectum comprises a slender pointed prong broadly shouldered at its base and with a slender incurved tooth projecting anteriorly from each shoulder (Fig. 35I). The chelicera is shown in figure 35J. Although the dentition of both digits is similar to that of *magnus*, the fixed digit is more slender and lacks the basal protuberance, and the movable digit is shorter

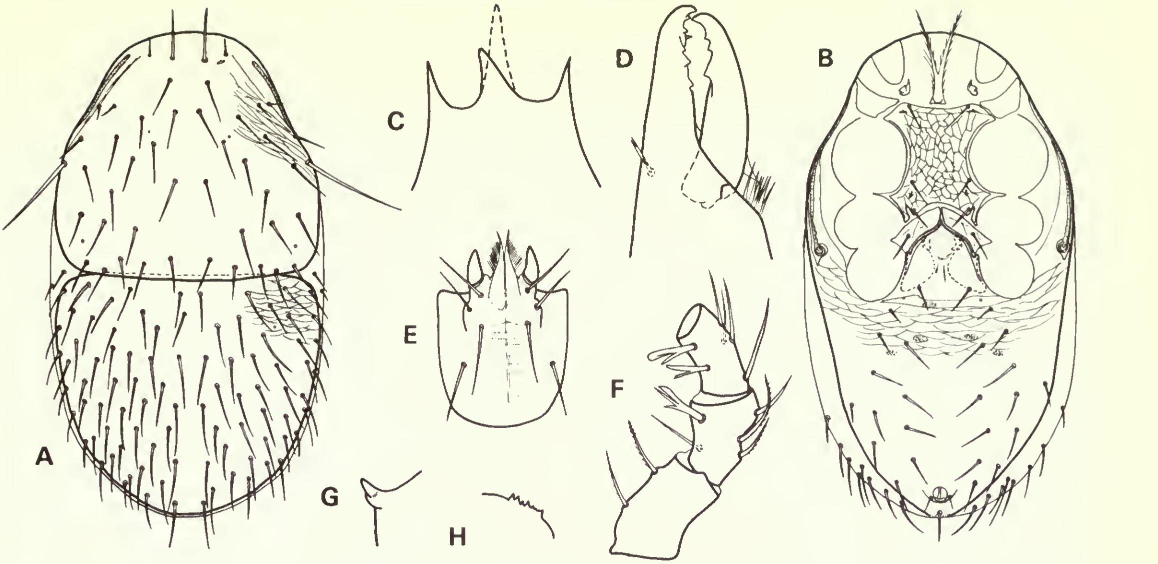

Fig. 36 *Eugamasus berlesei* Willmann, **female** – A dorsum; B venter; C tectum; D chelicera; E venter of gnathosoma; F palp trochanter, femur and genu; G dorsal spur of coxa I; H anterior margin of coxa of leg III.

(120 μm). The chaetotaxy of the palp trochanter, femur and genu is shown in figure 35K. The venter of the gnathosoma is as in figure 35L. It bears a pair of protuberances adjacent to the palpcoxal setae similar to those of *magnus.* Leg II, shown in detail in figure 35M, is considerably less heavily armed than in *magnus.* The chaetotaxy of leg I (*c.* 1300 μm), leg III (*c.* 850 μm) and leg IV (*c.* 1300 μm) are essentially as in *magnus,* but trochanter IV lacks the small dorsal protuberance.

Female. The podonotal shield (600–700 μm long × 624–660 μm wide) is reticulated mainly around the lateral and posterior margins. It bears 23 pairs of slender simple setae of which *r3* are long (Fig. 36A). The opisthonotal shield (564–660 μm long × 636–708 μm wide) is entirely reticulated and bears 40–50 pairs of simple setae. In the specimen figured the right side has less setae than the left.

The tritosternum has a narrow base and pilose laciniae and the small presternal shields are characteristically shaped (Fig. 36B). The sternal shield is entirely reticulated and the setae are simple. The metasternal setae are also simple. The genital shield is pointed anteriorly and bears a pair of small lateral horns. The single pair of genitals and the 11–12 pairs of opisthogastric setae are simple. The postanal seta is longer than the paranals. The nine or so pairs of setae on the interscutal membrane are also simple. The peritreme extends to coxa I.

The tectum of the specimen figured is quite a common variation although the symmetrical form shown dotted is more normal (Fig. 36C). The chelicera is as in figure 36D. The venter of the gnathosoma is shown in figure 36E: the setae are simple. The chaetotaxy of the palp trochanter, femur and genu is as in figure 36F. The setae of leg I are fine and slender: the coxa bears distally a conspicuous but small conical dorsal spur (Fig. 36G). Leg II bears stout ventral setae on the femur, genu, tibia and tarsus. Leg III bears similar but slightly less stout ventral setae, whilst on the coxa there is usually a conspicuous anterior sclerotized ridge which is either finely toothed (Fig. 36H) or plain. Leg IV also bears stout ventral setae on the genu, tibia and tarsus.

Material examined. 57 samples – 14 DNN, 15 ♂♂, 69 ♀♀.

England: Devon, Somerset, Hampshire, Surrey, Kent, Buckinghamshire, Oxfordshire, Hertfordshire, Huntingdonshire, Cambridgeshire, Norfolk, Suffolk, Derbyshire, Lancashire, Westmorland, Yorkshire.

WALES: Monmouthshire.
SCOTLAND: Roxburghshire, Midlothian, E. Lothian, Perthshire, Angus, Isle of Mull.
IRELAND: Kerry, Clare.

The British material examined has been collected from a wide variety of habitats, e.g. deciduous and coniferous litter, mosses, rotten logs, in caves, on small mammals (mole *Talpa europaea* L. and field vole *Microtus agrestis* (L.)) and in moles' nests.

DISTRIBUTION. Previous British records of *magnus* Kramer are probably all referrable to the present species. Halbert (1915) records *magnus* Kramer *teste* Berlese, 1906, from Westport, Co. Mayo, but the single specimen examined is a female of *Vulgarogamasus kraepelini*. Hull (1918) records *magnus* Kramer from Northumberland and Durham, but a single female without data in the Hull Collection is *berlesei*. Turk (1944) records *magnus* Kramer from caves in the Mendip Hills of Somerset, but a male and female examined from this collection are *berlesei*. *Eugamasus anglocavernarum* Turk, 1944, which was described from a single male, has been examined by me and I agree with Micherdzinski (1969) in synonymizing it with *berlesei*. Hazelton's (1970*a*) and Turk's (1972) records of a female *anglocavernarum* from Swanley, Kent, are probably referrable to *berlesei*, but the specimen was not available for examination, whilst Turk's (1967) mention is probably based on his 1944 material. Further records from caves are from Somerset (Hazelton, 1967*c*, 1968*b*, *c*, 1970*b*), Breconshire (Hazelton, 1970*a*, 1971*b*), Derbyshire and Yorkshire (Hazelton, 1972).

Abroad *Eugamasus berlesei* is recorded from Belgium (Willmann, 1935, Leruth, 1939, van Daele & Heungens, 1974), Germany (Holzmann, 1969, Karg, 1965, 1971), Poland (Micherdzinski, 1969), Austria (Leitner, 1946), Switzerland (Cooreman, 1954, 1959, Schweizer, 1961), Italy (Berlese, 1906) and Western Siberia (Davydova, 1976).

Eugamasus cavernicola Trägårdh

(Fig. 37A–H)

Eugamasus magnus var. *cavernicola* Trägårdh, 1912: 524.
Eugamasus magnus var. *trägårdhi* Oudemans, 1913*b*: 373, *nom. nov. pro Eugamasus magnus* var. *cavernicola* Trägårdh, 1912, non *Eugamasus magnus* var. *cavernicola*, Berlese, 1909* = *Parasitus loricatus* (Wankel) auctt. and non *Parasitus traegardhi* Micherdzinski, 1969: 567 = *Parasitellus talparum* (Oudemans).
Parasitus cavernicola (Trägårdh). Micherdzinski, 1969: 526.
Parasitus cavernicolus: Karg, 1971: 449.
Parasitus (Eugamasus) cavernicola: Bregetova *et al.*, 1977: 67.
Eugamasus cavernicola: Holzmann, 1969: 16. Athias-Henriot, 1979: 7.

For the time being, at least until more material including deutonymphs and males has been collected, I am following Karg (1971) in the separation of *Parasitus cavernicola* (Trägårdh) and *monticola* (Berlese, 1906: 179). The British specimens examined (four females) key down to *cavernicolus* (*sic*) in Karg and either *monticola* or *cavernicola* in Holzmann, but match closest the figures of *cavernicola* given first by Holzmann and then copied by Karg. Whatever the outcome of further collecting and possible rearing, at present only one species, here referred to as *Eugamasus cavernicola* Trägårdh, is recorded from the British Isles.

DEUTONYMPH AND MALE. See remarks above.

FEMALE. The podonotal shield (508–564 μm long × 552–600 μm wide) is entirely reticulated and bears 21 pairs of simple setae of which *r3* (*c.* 210 μm) are the only relatively long pair (Fig. 37A). The opisthonotal shield (504–552 μm long × 564–588 μm wide) is also entirely

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*The name *Eugamasus magnus* var. *cavernicola* Berlese, 1909, first appears in the literature in Oudemans, 1913*b*: 373 and again in 1914, Heft 8: 116. It has subsequently been quoted by several authors, including Micherdzinski, 1969: 552, but it does not appear to have been published by Berlese. This is explained in a letter I have received from Dr Fausta Pegazzano dated 1 April 1977 in which she quotes from a manuscript catalogue compiled by Berlese as follows: '*Eugamasus magnus* (Kram.) Berl. var. *cavernicola* (Berl.) Oud. (Oudemans, 1913, *Ent. Ber.* 3: 373, *nomen mutavit* = var. *trägårdhi*)'. Oudemans (1913*b*) appears to refer to correspondence he had with Berlese in 1909 as there are in Florence specimens labelled '*E. magnus* var. *cavernicola*' collected at Maastricht, Netherlands.

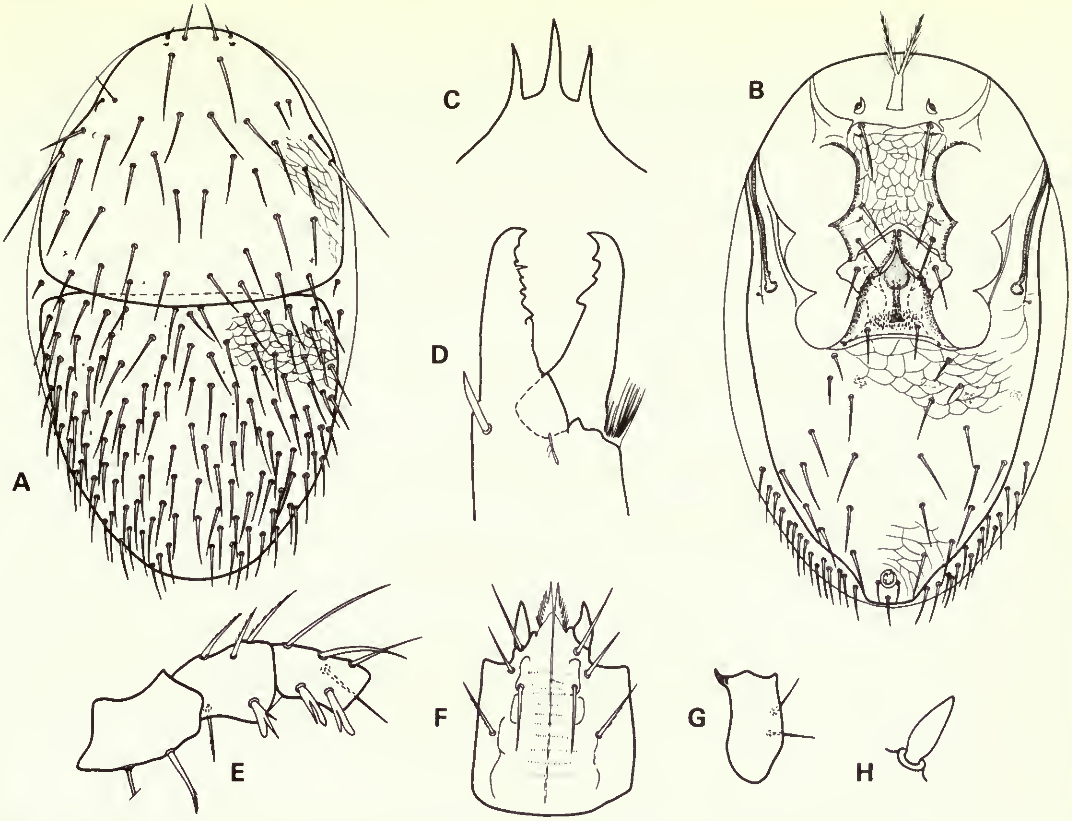


Fig. 37 *Eugamasus cavernicola* Trägårdh, **female** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma; G coxa of leg I; H ventral seta of femur of leg II.

reticulated. It bears about 60 pairs of simple setae whose distribution, whilst being fairly even, is not entirely symmetrical.

The tritosternum has a narrow base and pilose laciniae and is flanked by a pair of small crescent-shaped presternal shields (Fig. 37B). The sternal shield is somewhat narrow and is evenly reticulated. The genital shield is pointed anteriorly and bears small teeth at the 'shoulders'. The opisthogastric shield is evenly and strongly reticulated and bears eleven pairs of simple setae. The paranal setae are shorter than the postanal. The posterior interscutal membrane bears about fifteen pairs of simple setae. The peritreme extends to coxa I.

The tectum (Fig. 37C) comprises three simple slender prongs. The chelicera is shown in figure 37D, the chaetotaxy of the palp trochanter, femur and genu in figure 37E, and the venter of the gnathosoma in figure 37F. The setae on leg I are the finest, whilst those on legs II–IV are generally only slightly stouter. Coxa I bears anterodorsally a small curved spur (Fig. 37G). Femur II bears ventrally a single stout peg-like seta which arises from a small tubercle (Fig. 37H).

MATERIAL EXAMINED. 3 samples – 4 ♀♀.

ENGLAND: One female from the nest of a mole *Talpa europaea* L. near Froxfield, Wiltshire, 29 January 1964 and two females from beech/oak litter at Sutton Bonington, Leicestershire, in the 1960s.

SCOTLAND: One female from a mole's nest Midlothian/Roxburghshire border area, 1964.

Distribution. This species has not previously been authentically recorded from the British Isles. *Eugamasus magnus* var. *monticola* has been recorded by Turk (1944, 1972) who examined two females from caves in the Mendip Hills of Somerset, two females from Co. Cork and one adult from Yorkshire and assigned them to this taxon. Unfortunately specimens could not be located for examination. Similarly, Turk's (1967) records of *monticola* and *tragardhi* have not been substantiated, nor have those of Hazelton (1967*a*, 1970*b*) from Surrey, Hazelton (1967*c*) from Somerset, and Hazelton (1972) from Yorkshire.

Other recorded occurrences for both *cavernicola* and *monticola* are mainly from caves and are as follows:

a, *cavernicola:* France (Trägårdh, 1912, Cooreman, 1959), Belgium (Willmann, 1935, Leruth, 1939), Germany (Willmann, 1938*b*, Holzmann, 1969, Karg, 1971), Switzerland (Cooreman, 1959), Hungary (Cooreman, 1951), Jugoslavia (Willmann, 1941) and Romania (Cooreman, 1951).

b, *monticola:* Germany (Holzmann, 1969, Karg, 1971) and Italy (Berlese, 1906). The record given by Schweizer (1961: 26) refers to the female of *E. berlesei q. v.*

Eugamasus crassitarsis (Halbert)
(Fig. 38A–N)

Gamasus (Eugamasus) crassitarsis Halbert, 1923: 363.
Parasitus crassitarsis: Micherdzinski, 1969: 508. Karg, 1971: 450.
Parasitus (Eugamasus) crassitarsis: Tichomirov, 1969: 1475. Bregetova *et al.,* 1977: 72.
Eugamasus crassitarsis: Athias-Henriot, 1979: 7.

Deutonymph. Unknown.

Male. The finely reticulated dorsal shield (1560–1770 μm long × 960–1044 μm wide) is entire, but the transverse suture extends almost to the lateral margins (Fig. 38A). Twenty-three pairs of simple setae are present on the podonotal region, the only long pair being *r3*. The opisthonotal region bears about 55 pairs of simple setae arranged very nearly symmetrically.

The tritosternum has a long base and pilose laciniae. The sternogenital setae are simple as are the symmetrically arranged 20 or more pairs of opisthogastric setae (Fig. 38B). The three anal setae are fine, short and of equal length. The peritreme extends to the level of coxa I.

The tectum (Fig. 38C) comprises three pointed prongs, the central one being long and parallel sided, the two lateral ones very short. The chelicera is as in figure 38D. The palp trochanter, femur and genu are shown in figure 38E: the anterolateral seta on the femur is five-tined whilst the two anterolateral setae on the genu are bifid. The corniculi are bold, stalked and slightly diverging (Fig. 38F): the gnathosomal setae are simple and up to 12 rows of hypognathal denticles are visible. Leg II is shown in detail in figure 38G: the inflated but finely attenuated spine on the tarsus frequently has the filamentous part broken off (see Schweizer, 1961, fig. 26*c*).

Female. The podonotal shield (768–800 μm long × 696–732 μm wide) bears 23 pairs of setae and, like the male, only *r3* are long. The opisthonotal shield (672–800 μm long × 684–880 μm wide) bears over 50 pairs of setae arranged almost symmetrically. Both shields are finely reticulated over their entire surfaces (Fig. 38H). The posterior interscutal membrane bears half a dozen or so simple setae.

The tritosternum has a narrow base and pilose laciniae. It is flanked by a pair of characteristically shaped presternal shields (Fig. 38I). The sternal and metasternal shields are granular with faint reticulations. The posterior margin of the sternal shield is irregularly concave. The sternal, metasternal and genital setae are simple. The genital shield is pointed anteriorly and bears a pair of prominent lateral teeth. The main features of the endogynium are shown through the genital shield. The strongly reticulated opisthogastric shield bears 12 pairs of simple setae and the posterior membrane from seven to 10 setae on each side that are not always paired. The postanal seta is longer than the paranals. The peritreme extends anteriorly to the level of coxa I.

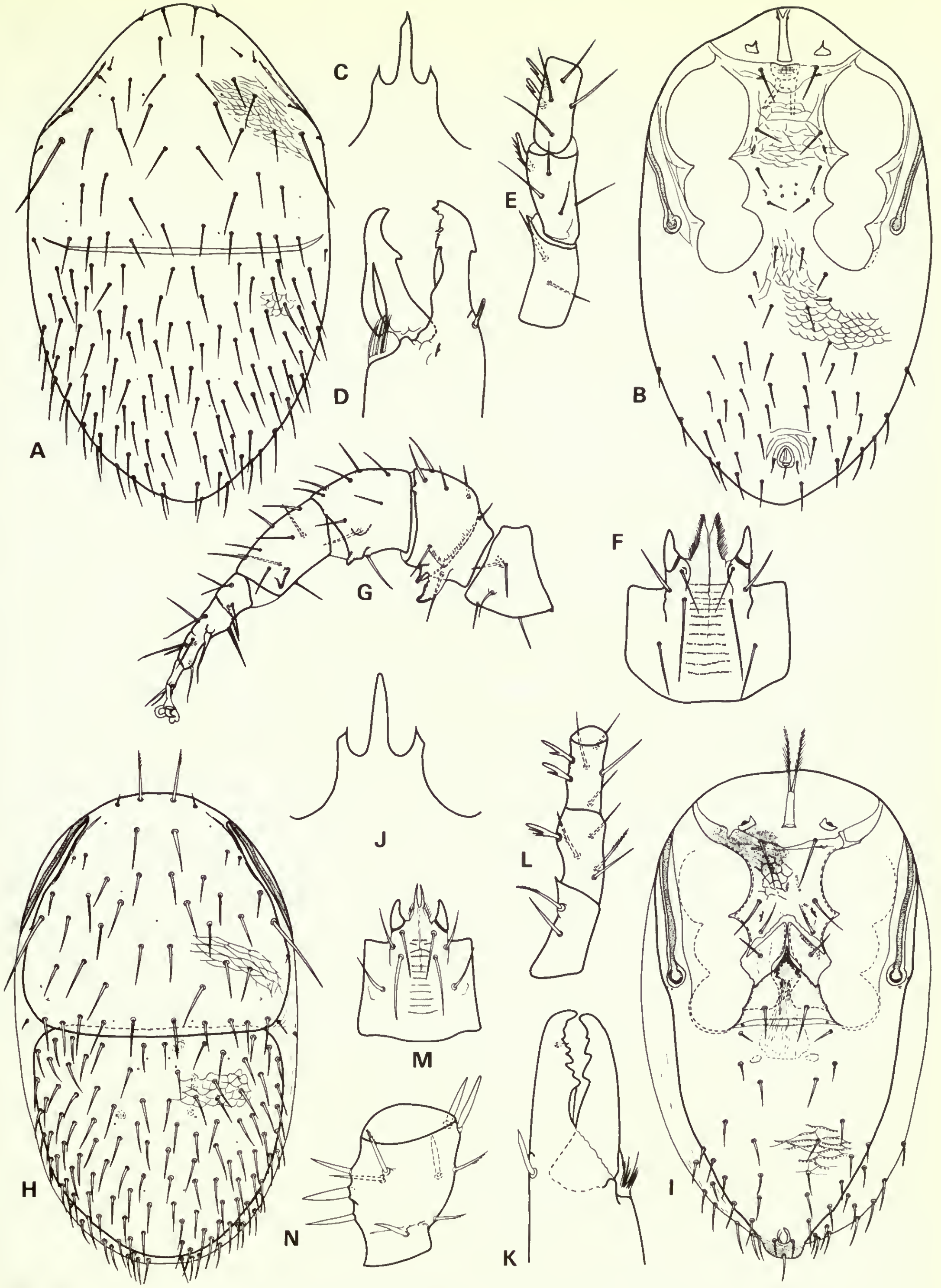


Fig. 38 *Eugamasus crassitarsis* (Halbert), **male** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma; G leg II: **female** – H dorsum; I venter; J tectum; K chelicera; L palp trochanter, femur and genu; M venter of gnathosoma; N femur of leg II.

The tectum (Fig. 38J) is almost identical to that of the male. The chelicera is shown in figure 38K, and the palp trochanter, femur and genu in figure 38L. The venter of the gnathosoma is shown in figure 38M: the setae are simple. All setae on the legs are simple, or at the most, traces of pilosity are just discernible. A number of the ventral setae are stouter and clearly smooth, for example on trochanter and femur I, femur – tarsus II, trochanter – tarsus III and IV. Femur II is shown in figure 38N.

MATERIAL EXAMINED. 17 samples – 9 ♂♂, 9 ♀♀.

ENGLAND: Gloucestershire, Hampshire, Surrey, Berkshire, Hertfordshire, Lancashire, Yorkshire, Northumberland.

IRELAND: Wexford, Kildare, Dublin, Meath, Mayo.

All samples comprise single specimens except the Hampshire one which comprises one male and one female.

This large, scarce, species was originally described (Halbert, 1923) from two males found under a stone on the seashore at high tide mark in Co. Wexford, 12 March 1922. I have examined two males on slides in the Halbert Collection, one labelled according to Halbert's description, the other labelled 'Glasnevin [Dublin], amongst soil, 31.3.'22' in Halbert's writing. Fresh material examined is from grass cuttings, leaf litter (mainly oak), arable land, pasture on sandy soil, grass on chalk, barley on sandy soil and mossy coniferous litter.

DISTRIBUTION. Previous British records are those of Halbert (1923) and a more recent record by Curry (1969) from grassland in Co. Kildare.

It is recorded from Belgium (van Daele & Heungens, 1974), Germany (Karg, 1971), Switzerland (Schweizer, 1961) and Poland (Micherdzinski, 1969).

Genus ***PORRHOSTASPIS*** Müller

Porrhostaspis Müller, 1859. *Lotos* **9:** 28.

TYPE SPECIES *Porrhostaspis lunulata* Müller, 1859.

Dorsal shield of male entire, with transverse suture; female and deutonymph with separate podonotal and opisthonotal shields. Setae *z5* of dorsal hexagon longest and strongest in the deutonymph and female, scarcely different from *j5* and *j6* in the male. Tritosternum biramous in deutonymph and adults. Junction between sternal and metasternal shields in female oblique. Genital shield of female elongate, tricuspid anteriorly. Opisthogaster of female bearing about 15 pairs of setae, male and deutonymph with about 14 and 20 pairs respectively. Seta *al* of palp femur spiculate on one margin; setae al_1 and al_2 of palp genu entire, spatulate. Male chelicerae asymmetrical due to presence of variable digitiform process on the spermatodactyl of the right chelicera. Corniculi in the deutonymph and female short, entire; in the male longer; cleft on the inner margin. Legs of deutonymph and female without spurs; only leg II of male spurred. Lobes of pulvilli normal, rounded.

Porrhostaspis lunulata Müller
(Figs 39A–P; 40A–H)

Porrhostaspis lunulata Müller, 1859: 29. Samšiňák, 1960: 275. Evans & Till, 1979: 209.
Eugamasus lunulatulus (sic): Schweizer, 1961: 30.
Eugamasus lunulatus: Hirschmann, 1957: 15, III. Holzmann, 1969: 17.
Parasitus lunulatus: Micherdzinski, 1969: 455. Karg, 1971: 449.
Parasitus (Eugamasus) lunulatus: Tichomirov, 1969: 1475. Bregetova *et al.*, 1977: 62, 67.
Paracarpais (Eteocarpais) lunulata: Athias-Henriot, 1978: 48.
Gamasus cornutus G. & R. Canestrini, 1882: 48.
Parasitus cornutus: Oudemans, 1902*b*: 34.

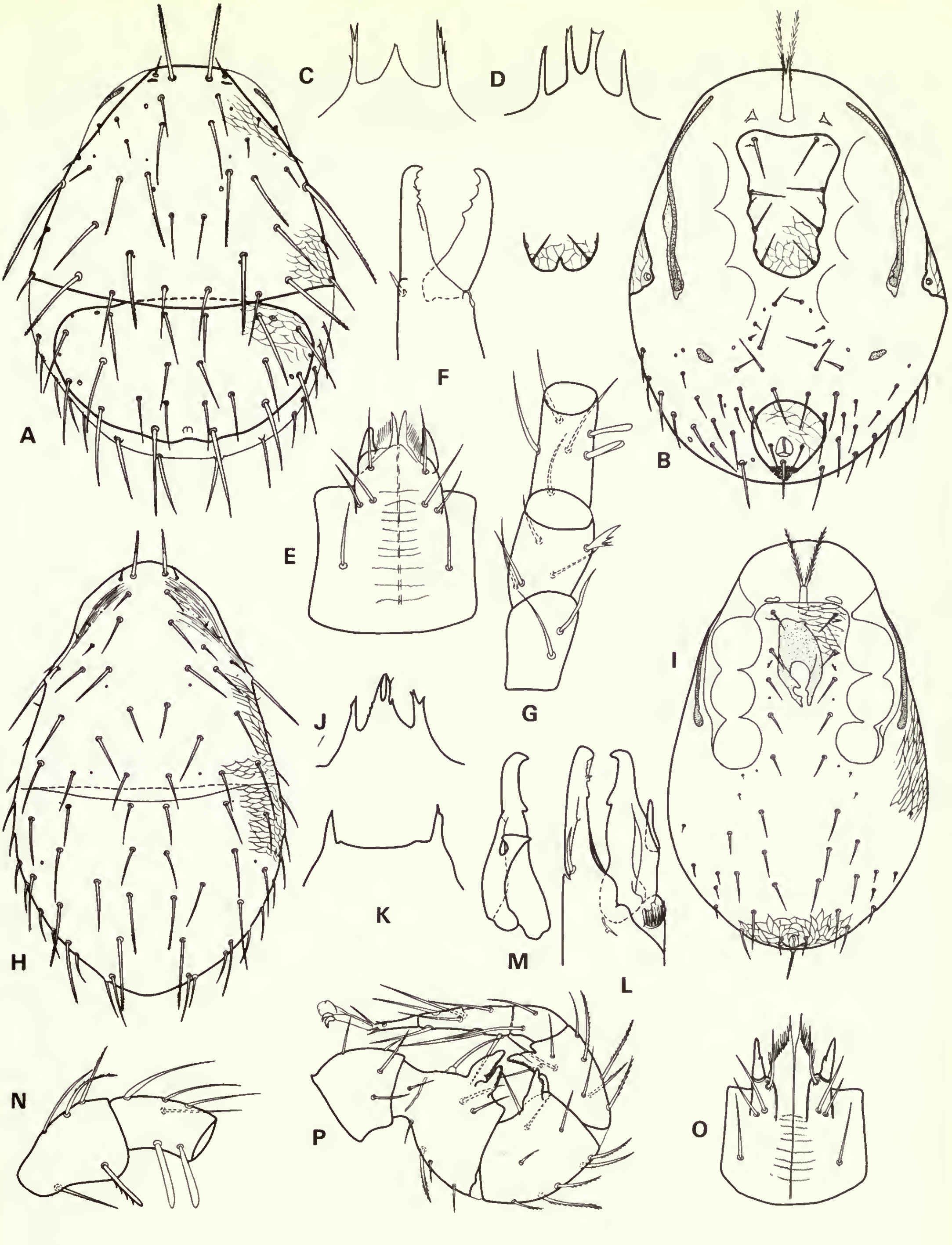


Fig. 39 *Porrhostaspis lunulata* Müller, **deutonymph** – A dorsum; B venter; C, D tectum; E venter of gnathosoma; F chelicera; G palp trochanter, femur and genu: **male** – H dorsum; I venter; J tectum (typical); K tectum (extreme variation); L right chelicera (typical); M movable digit of right chelicera (variation); N palp femur and genu; O venter of gnathosoma; P leg II.

Gamasus (Eugamasus) cornutus: Berlese, 1906: 173.
Eugamasus epsilon: Oudemans & Voigts, 1904 in Voigts & Oudemans, 1904: 654.
Parasitellus ferox (Trägårdh, 1910) sensu Turk & Turk, 1952: 478 = *Porrhostaspis lunulata* (Müller, 1859) and *Parasitus loricatus* (Wankel, 1861), non Trägårdh, 1910 = *Parasitellus fucorum* (De Geer, 1778).

DEUTONYMPH. In this species the deutonymph is, in contrast to the adults, generally very weakly sclerotized and frequently the dorsal shields and the sternal shield are rather irregularly formed. The podonotal shield (360–450 μm long × 560–570 μm wide) is finely reticulated and bears 19 pairs of setae, most of which are long and broad with fine pilosity (Fig. 39A). The opisthonotal shield (240–275 μm long × 432–470 μm wide) is also finely reticulated. It bears 10 pairs of long setae, and the surrounding membrane between five and eight pairs, the posterior two of which are the longest.

The tritosternum, which has a narrow base and pilose laciniae, may be flanked by a pair of small triangular presternal shields (Fig. 39B). The sternal shield is reticulated and may be indented posteriorly (see inset to the figure). The sternal setae become progressively shorter from I–IV. The anal shield is circular with a posterior taper and the postanal seta is the longest. The opisthogastric membrane bears from 16 to over 20 pairs of setae, those surrounding the anus being the longest. Faint metapodal shields are sometimes present. The peritreme extends to coxa I.

Two forms of tectum are shown in figures 39C and D. The venter of the gnathosoma is as in figure 39E, the chelicera in figure 39F, and the chaetotaxy of the pedipalp in figure 39G. The leg setae are generally long and simple, although some are very finely pilose. Tarsus IV bears a long seta (*c.* 67 μm) dorsally.

MALE. The male of this species is one of the most heavily sclerotized members of the Parasitinae. The dorsum is completely covered by a dark yellowish-brown reticulated shield which is divided by a transverse suture running almost the full width of the idiosoma and results in the anterior portion often overlapping the posterior (Fig. 39H). The idiosoma averages 948–1100 μm long × 630–800 μm wide. The podonotal region bears 21 pairs of setae distributed as illustrated. Their lengths appear constant, in contrast to the female where considerable variation has been observed. The opisthonotal region bears 20 pairs of setae which also show almost no variation. Many of the longer setae are extremely finely pilose for much of their length.

The tritosternum has a narrow base and pilose laciniae. It is flanked by a pair of elliptical presternal shields. The genital lamina is characteristically shaped and often appears to be haphazardly situated beneath the anterior half of the sternogenital shield (Fig. 39I). The sternogenital setae are simple. The entire venter is strongly sclerotized and bears, posterior to coxae IV, 14 pairs of setae in addition to those associated with the anus. Several pairs are extremely short and their location is shown in the figure. The paranal setae are fine and are just over half the length of the stouter postanal seta. The peritreme extends anteriorly to the level of coxa I or slightly beyond.

A typical tectum is illustrated in figure 39J. However, there is a range of variation and an extreme form is shown in figure 39K. The male chelicerae in this species are unusual in that the right spermatodactyl has a digitiform protuberance which is usually smoothly tapered (Fig. 39L), although occasionally shaped otherwise (Fig. 39M). The left spermatodactyl is smooth and without trace of irregularity. The chaetotaxy of the palp femur and genu is as in figure 39N. The stalked corniculi are straight and narrow and are notched on the inner margin (Fig. 39O). The gnathosomal setae are simple. Leg II is shown in detail in figure 39P. No significant variation has been encountered. Most of the other leg setae are long and many are extremely finely pilose.

FEMALE. The reticulated podonotal shield (504–576 μm long × 588–756 μm wide) bears 21 pairs of setae of which the majority are long, but not constantly so, and very finely pilose, the longest, *r3* being up to 240 μm (Fig. 40A). The opisthonotal shield (432–540 μm

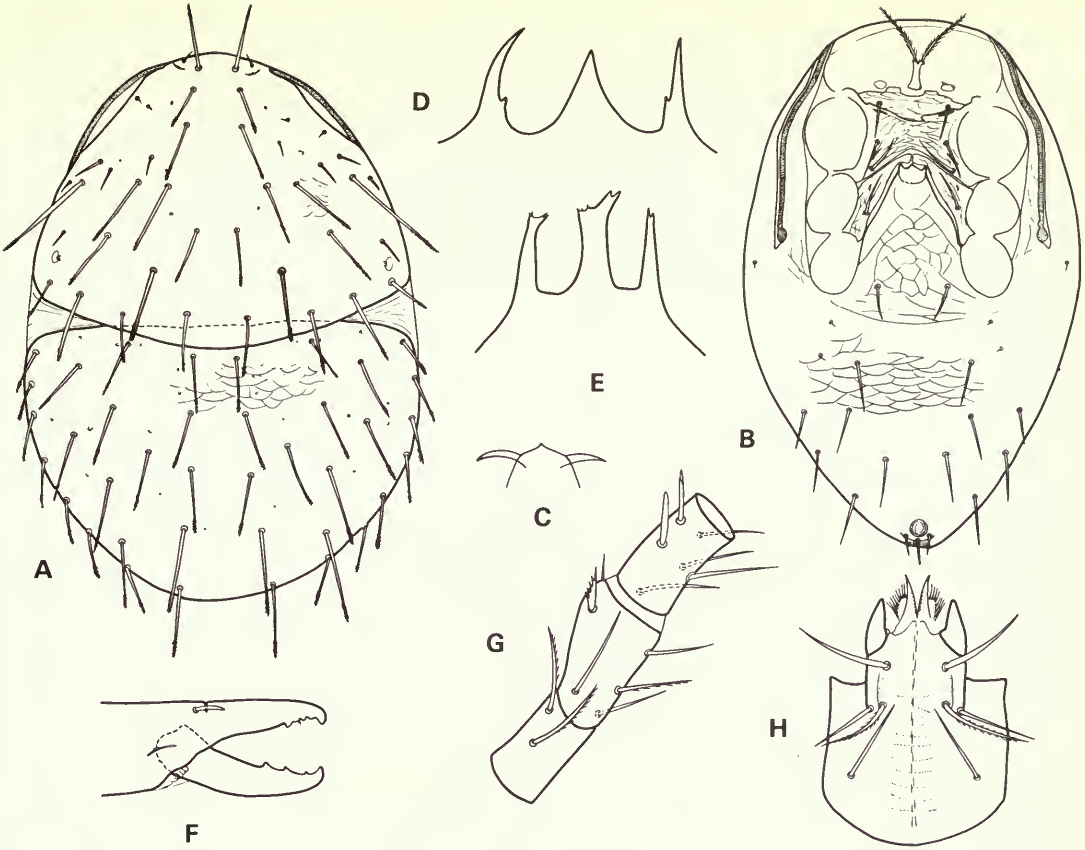


Fig. 40 *Porrhostaspis lunulata* Müller, **female** – A dorsum; B venter; C apex of genital shield showing extreme variation; D, E tectum; F chelicera; G palp trochanter, femur and genu; H venter of gnathosoma.

long × 552–708 μm wide) is also completely reticulated. It bears 19 pairs of long setae, mainly very finely pilose.

The tritosternum has pilose laciniae and a narrow base. It is flanked by a pair of small but conspicuous presternal shields. The short sternal shield is normally not evenly sclerotized, the portion anterior to the first pores, and bearing setae I, being more lightly sclerotized than the remainder (Fig. 40B). The metasternal shields are obliquely narrowed, their setae being more slender than the sternals. The genital shield is broad and long and its apex is normally trispinate. Considerable variation occurs in the outline of the apex, the trident often being malformed or missing. An extreme variation is shown in figure 40C, a specimen in the J. E. Hull collection from Hylton, Co. Durham. The genital setae are slender and simple. The opisthogastric shield bears eight pairs of setae, two posterior to coxae IV being minute, the remainder long. The surrounding membrane bears generally seven pairs of setae. The postanal seta is longer than the paranals. The peritreme extends anteriorly to coxae I.

The tectum is broad and trispinate, but shows considerable variation in the form of the tines (Figs 40D, E). The chelicera is shown in figure 40F, and the chaetotaxy of the palp trochanter, femur and genu in figure 40G. The four pairs of gnathosomal setae are of approximately equal length and stoutness, but the internal posterior hypostomatics are finely pilose (Fig. 40H). Eleven rows of hypognathal denticles are usually clearly defined. The leg setae are mainly long and many are extremely finely pilose.

MATERIAL EXAMINED. 142 samples –21 DNN, 70 ♂♂, 163 ♀♀.

ENGLAND: Isles of Scilly, Cornwall, Devon, Somerset, Dorset, Gloucestershire, Steep Holm

(Bristol Channel), Isle of Wight, Hampshire, Sussex, Surrey, Kent, Buckinghamshire, Middlesex, Hertfordshire, Essex, Suffolk, Cambridgeshire, Leicestershire, Nottinghamshire, Warwickshire, Staffordshire, Worcestershire, Cheshire, Lancashire, Westmorland, Cumberland, Yorkshire, Northumberland, Durham.
WALES: Monmouthshire, Glamorganshire, Caernarvonshire.
SCOTLAND: Roxburghshire, Midlothian, East Lothian, Dunbartonshire, Perthshire, Argyllshire, Inverness-shire, Inner Hebrides (Eigg), Outer Hebrides (St Kilda).
IRELAND: Kildare, Clare, Mayo, Sligo.
CHANNEL ISLANDS: Jersey.

This widespread European species is distributed throughout the British Isles and is found in a wide range of habitats and situations. Leafmould, flood debris and mosses, under bark, in grassland, compost and mushroom beds are the more frequent biotopes. I have examined one deutonymph from seaweed. There are several records from the fur of *Apodemus sylvaticus* (L.) and one is from a 'baby bat', Devon, 14 July 1963, coll. A. J. Sutcliffe, but this species has not normally been encountered as a nest inhabitant in this country. Turk (1972) records it from caves. It has been recorded from small mammals in Czechoslovakia (Mrciak & Rosický, 1956, Rupeš, 1965) and Poland (Willmann, 1952*b*), whilst Cooreman (1960) has recorded it from bat guano in Afghanistan.

DISTRIBUTION. Previous British records are from Co. Dublin (Halbert, 1915), the Tyne Province and Scotland (no precise locality) (Hull, 1918), Isle of Lewis, Outer Hebrides (Hora, 1934), the Inner Hebrides (Bertram, 1939), the Channel Islands (Browning, 1956), South Wales (Bhattacharyya, 1962), Buckingham Palace Garden (Bristowe, 1964), Westmorland (Block, 1965), Co. Kildare (Curry, 1969), Huntingdonshire (Davis, 1970), Somerset and Surrey (Turk, 1972), Somerset (Hazelton, 1971*a, b*), and Devon, Breconshire and Shropshire (Hazelton, 1971*b*). The record of *Parasitellus ferox* (Trägårdh) from the Isle of Wight (Turk & Turk, 1952) is referrable to the present species.

It is recorded from Iceland (Sellnick, 1940), Finland (Nordberg, 1936), Holland (Oudemans, 1902*b*), Belgium (Willmann, 1935, Leruth, 1939, Cooreman, 1943, van Daele & Heungens, 1974, 1975), France (Cooreman, 1959), Germany (Voigts & Oudemans, 1905, Poppe, 1906, Schweizer, 1926, Holzmann, 1969, Karg, 1965, 1971), Switzerland (Schweizer, 1949, 1961), Italy (G. & R. Canestrini, 1882, Berlese, 1906, Valle, 1955, Cooreman, 1959), Austria (Franz, 1943, Leitner, 1946), Czechoslovakia (Müller, 1859, 1860, Vitzthum, 1925, Pax & Maschke, 1935, Willmann, 1954, Mrciak & Rosický, 1956, Halašková, 1959, Rupeš, 1965), Poland (Schweizer, 1925, Willmann, 1952*b*, Micherdzinski, 1969), the U.S.S.R. (Bregetova, 1956), and Afghanistan (Cooreman, 1960).

Genus *CORNIGAMASUS* Evans & Till

Cornigamasus Evans & Till, 1979. *Trans. zool. Soc. Lond.* **35:** 209.

TYPE SPECIES. *Gamasus coleoptratorum* var. *lunaris* Berlese, 1882*a*.

Dorsal shield of male entire, with transverse suture; female and deutonymph with separate podonotal and opisthonotal shields. Setae *z5* of dorsal hexagon different in form from *j5* and *j6*. Tritosternum of male absent, that of deutonymph and female biramous. Junction between metasternal and sternal shields of female oblique. Genital shield of female subtriangular. Opisthogaster usually with less than 15 pairs of setae. Seta *al* of palp femur setose, at most spiculate distally; setae al_1 and al_2 of palp genu spatulate. Male chelicerae symmetrical. Corniculi long, slender, parallel, extending beyond anterior margin of palp trochanter, grooved to accommodate 'salivary' styli. Legs of deutonymph and female without spurs; only leg II of male with spurs. Lobes of pulvilli normal, rounded.

Cornigamasus lunaris (Berlese)
(Fig. 41A–N)

Gamasus coleoptratorum var. *lunaris* Berlese, 1882*a*: 125.

Gamasus fucorum var. *lunaris* Berlese, 1882*b*: 640.
Gamasus (Gamasus) lunaris: Berlese, 1906: 147.
Parasitus lunaris: Sellnick, 1940: 23. Schweizer, 1961: 17. Micherdzinski, 1969: 437. Karg, 1971: 446.
Parasitus (Coleogamasus) lunaris: Tichomirov, 1969: 1476. Bregetova *et al.*, 1977: 85, 89.
Eugamasus lunaris: Holzmann, 1969: 14.
Cornigamasus lunaris: Evans & Till, 1979: 209.
Parasitus spinipediformis Trägårdh, 1904: 37. Micherdzinski, 1969: 437.

DEUTONYMPH. The reticulated dorsal shields are strongly sclerotized and are usually a rich yellowish-brown in colour. The posterior margin of the podonotal shield is convex medially and the protrusion fits closely into the concave anterior margin of the opisthonotal shield (Fig. 41A). The podonotal shield (384–430 μm long × 312–379 μm wide) bears 18 pairs of setae, none of which is long or stout. Setae *j1, z5* and *r3* are up to 45 μm long and the remainder up to 38 μm. A narrow band of cuticle is situated across the anterior margin of the shield. The opisthonotal shield (156–197 μm long × 264–324 μm wide) bears 12 pairs of setae of which *J5* and *Z3* are a little stouter than the remainder and are finely pilose distally.

The tritosternum has long laciniae and is flanked by strong elongate presternal shields. The sternal shield (*c.* 245 μm long) is strongly sclerotized and is broad and convex anteriorly (Fig. 41B). The anal shield is elliptical and the anal setae are of equal length. Small metapodal shields are conspicuous and the opisthogastric membrane bears simple setae. The peritreme extends anteriorly to the level of coxa I.

The tectum is shown in figure 41C. The chelicera bears a lateral tooth on the fixed digit (Fig. 41D). The rest of the gnathosoma, the corniculi and the ventral setae, and the chaetotaxy of the pedipalp are the same as in the adults (Figs 41L, M). The anterolateral seta on the palp femur is not modified, but those of the genu are broad and spatulate distally. All leg setae are simple although a few, mainly on tarsi II–IV, are strong. Coxa III bears in this stage, and also in the adults, a small tubercle (Fig. 41N).

MALE. The idiosoma is completely sclerotized although dorsally the podonotal region is separated from the opisthonotal region by a complete transverse suture which undulates as in the female (Fig. 41H). The anterior portion measures 408–420 µm long and the posterior 336–348 μm. The width is 396–408 μm. The dorsal chaetotaxy is as in the female with the addition, in the opisthonotal region, of setae that would otherwise be located on the membrane. Setae *j1, j4, z5, r3, Z1, Z3* and *J5*, and one additional posterior pair, are stout and pilose, the remainder being very fine and simple.

The tritosternum is absent (Fig. 41E). The genital lamina is flanked by a pair of sometimes fragmented presternal shields. The sternogenital setae are simple and the shield is separated from the opisthogastric region by a narrow suture. There are 11–14 or more pairs of setae in the opisthogastric region of which two pairs, flanking the anus, are stout and pilose. The three anal setae are short and fine. The peritreme extends to coxa I.

The tectum is as in the female (Fig. 41J). The chelicera is shown in figure 41F. The chaetotaxy of the pedipalp, the long corniculi (although slightly stalked in this sex), and the venter of the gnathosoma, are as in the female (Figs 41L, M). Leg II is shown in figure 41G. The setae of the remaining legs are simple. Coxa III bears, in common with the deutonymph and female, a small tubercle (Fig. 41N).

FEMALE. The podonotal shield (408–444 μm long × 384–432 μm wide) bears 21 pairs of setae. The majority are very short and fine, but *j1, j4, z5* and *r3* are long, stout and pilose. The posterior margin of the shield is undulating and convex medially, and closely abuts the concave anterior margin of the opisthonotal shield (Fig. 41H). The opisthonotal shield (372–384 μm long × 348–432 μm wide) bears 12 pairs of setae of which *Z1, Z3* and *J5* are long, stout and pilose.

The tritosternum has pilose laciniae and is flanked by a pair of wedge-shaped presternal shields (Fig. 41I). The sternal setae are of equal thickness, but the metasternals are more slender. The sternogenital region is not heavily sclerotized and the metasternal shields are often not clearly demarcated from the sternal shield. The genital shield is narrowly pointed

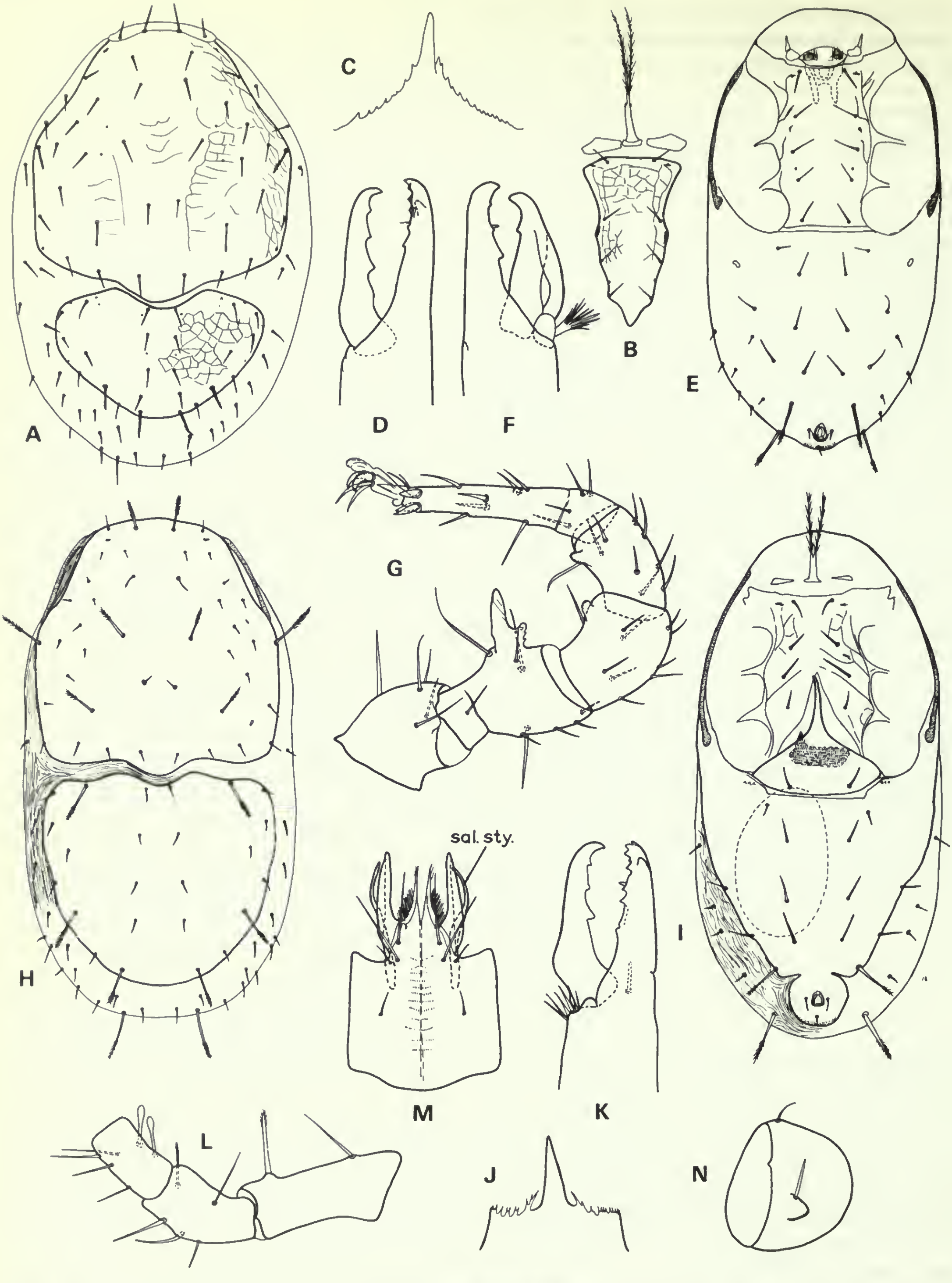


Fig. 41 *Cornigamasus lunaris* (Berlese), **deutonymph** – A dorsum; B sternal shield and tritosternum; C tectum; D chelicera: **male** – E venter; F chelicera; G leg II: **female** – H dorsum; I venter; J tectum; K chelicera; L palp trochanter, femur and genu; M venter of gnathosoma including 'salivary' styli, *sal. sty.*; N. coxa of leg III.

for half its length and the setae are simple. The most conspicuous part of the endogynium comprises a transversely situated granular band with a forward-protruding tongue on one side only. The tapered opisthogastric shield is often incised anterior to the anus. The opisthogastric shield bears seven pairs of setae, one pair immediately posterior to the genital shield is short, the remainder are longer with the pair nearest to the anus stout and pilose. The anal setae are short and fine. The opisthogastric membrane bears about four pairs of setae of which the posterior pair is also stout and pilose. The peritreme extends anteriorly to the level of coxa I.

The tectum (Fig. 41J) comprises a long smooth central prong emerging from a denticulate base. The chelicera is shown in figure 41K. Like the deutonymph, the fixed digit bears a lateral tooth, but in addition there is a small terminal tooth. The palp trochanter, femur and genu are shown in figure 41L and the venter of the gnathosoma in figure 41M. The corniculi are long and slender, reaching the midpoint of the palp femur. The leg setae are simple. Coxa III bears a small protuberance (Fig. 41N).

MATERIAL EXAMINED. 63 samples – 266 DNN, 38 ♂♂, 32 ♀♀.

ENGLAND: Cornwall, Isles of Scilly, Dorset, Hampshire, Sussex, Surrey, Kent, London, Middlesex, Hertfordshire, Essex, Norfolk, Cambridgeshire, Berkshire, Buckinghamshire, Cheshire, Lancashire, Northumberland.
WALES: Anglesey, and North Wales, no precise locality, see below.
SCOTLAND: Mull.
IRELAND: Clare, Kildare, Meath.

This species is found mainly in compost heaps, vegetable refuse, manure, haystacks and the like. Halbert (1915, 1920) records it from decaying seaweeds on the seashore but observes that this may not be its normal habitat.

DISTRIBUTION. Previous British records are from the Tyne Province and Cheshire (Hull, 1918), Co. Mayo (Halbert, 1915), Co. Dublin (Halbert, 1920), the Inner Hebrides (Bertram, 1939); and North Wales (Hill & Gordon, 1945) where the precise localities could not be published at the time. The material was from straw used to stuff the palliasses of American servicemen stationed in the area. The authors had been informed that *Parasitus lunaris* was a junior synonym of *Poecilochirus spinipes* (= *Gamasodes spiniger*), but apart from this being incorrect, I have examined a single deutonymph of *lunaris* from this collection.

It is recorded from Greenland (Trägårdh, 1904, Jorgensen, 1934), Iceland (Sellnick, 1940), Norway (Berlese, 1906), Sweden (Sellnick, 1958), Holland (Oudemans, 1913*c*), Belgium (van Daele & Heungens, 1974, 1975), Germany (Voigts & Oudemans, 1905, Karg, 1965, 1971, Holzmann, 1969), Austria (Leitner, 1946), Poland (Micherdzinski, 1969), Switzerland, (Schweizer, 1922, 1949, 1961), Italy (G. & R. Canestrini, 1882, Berlese, 1906), U.S.S.R.: Leningrad district (Vysockaja & Bregetova, 1957), Western Siberia (Davydova, 1969, 1976) and Israel (Shulov, 1957, Costa, 1966).

Genus ***PARASITELLUS*** Willmann

Parasitellus Willmann, 1939. *Abh. naturw. Ver. Bremen* **31**: 534.
Parasitus (Parasitus): Tichomirov, 1969. *Zool. Zh.* **48**: 1332.

TYPE SPECIES. *Eugamasus*(?) *ferox* Trägårdh, 1910 = *Acarus fucorum* De Geer, 1778.

Dorsal shield of male entire, with transverse suture; female and deutonymph with separate podonotal and opisthonotal shields. Setae *z5* of dorsal hexagon usually longer than *j5* and *j6*. Tritosternum normal, biramous, that of male not closely associated with genital orifice. Junction between sternal and metasternal shields of female oblique. Genital shield of female subtriangular. Opisthogaster with usually more than 40 pairs of setae. Setae *al* of palp femur usually strongly multifid, or at least pectinate; setae al_1 and al_2 of palp genu entire, spatulate. Male chelicerae symmetrical. Corniculi in the deutonymph and female short, entire, in the male longer, cleft on the inner margin. Legs of deutonymph and female without spurs; only leg II of male spurred. Lobes of pulvilli normal, rounded.

Parasitellus fucorum (De Geer)
(Figs 42A–N; 43A–F)

Acarus fucorum De Geer, 1778: 112.
Gamasus (Gamasus) fucorum: Berlese, 1906: 160.
Parasitus fucorum: Vitzthum, 1930*a*: 15. Schweizer, 1949: 14; 1961: 14. Colombo, 1961. Micherdzinski, 1969: 591. Holzmann, 1969: 28. Karg, 1971: 447. Davydova, 1976: 55.
Parasitus (Parasitus) fucorum: Tichomirov, 1969: 1476. Bregetova *et al.*, 1977: 72, 74.
Parasitellus fucorum: Evans & Till, 1979: 209.
Parasitus bomborum Oudemans, 1902*b*: 33; 1906: 237. Vitzthum, 1930*a*: 15.
Pergamasus bomborum: Voigts & Oudemans, 1905: 228.
Eugamasus(?) *ferox* Trägårdh, 1910: 395. Holzmann, 1969: 28.
Parasitellus ferox: Willmann, 1939*b*: 533. Non Turk & Turk, 1952: 478 = *Porrhostaspis lunulata* and *Parasitus loricatus.*
Gamasus bombianus Hull, 1917: 109. Micherdzinski, 1969: 591.
Gamasus nidicolens Hull, 1917: 110. Micherdzinski, 1969: 591.
Gamasus fucarius Hull, 1918: 86. Micherdzinski, 1969: 591.

DEUTONYMPH. The podonotal shield (492–516 μm long × 540–576 μm wide) is entirely covered by narrow reticulations and is strongly sclerotized (Fig. 42A). It bears 20 pairs of setae, *s2* being situated off the shield. Many of the setae are sparsely pilose at least on one margin. Setae *z5* and *r3* are the longest. The opisthonotal shield (336–360 μm long × 444–456 μm wide) is triangular in outline and bears 15 pairs of homogeneous setae which normally lack pilosity. Being considerably narrower than the podonotal shield, the opisthonotal is surrounded by a broad area of membrane and this is densely clothed with short simple setae.

The tritosternum has a narrow base and is flanked by a pair of angular presternal shields. The broad reticulated sternal shield (276–300 μm long) is conspicuously marked by fine striations, usually in its entirety, though sometimes with the portion anterior to sternal pores I clear (Fig. 42B). The four pairs of sternal setae, of which *st.* I are the finest, are pilose to a large degree. The anal shield is oval and reticulated with the postanal seta broader than the paranals. Granular elongate metapodal plates are present. The opisthogastric setae are relatively dense, similar to those on the dorsal membrane, but most are attached by small sclerotized plates, often barely larger than the setal bases. The peritreme extends to coxa I.

The tectum is shown in figure 42C, it varies in outline and may have a single tooth each side. The chelicerae bear very strong clear teeth (Fig. 42D). The chaetotaxy of the palp trochanter, femur and genu is as in figure 42E. The venter of the gnathosoma is shown in figure 42F, the corniculi are generally curved inwards at their tips. Most leg setae are strong and may be pilose at least in part. Tarsus IV has two conspicuous dorsal setae 300–320 μm in length (Fig. 42G).

MALE. The idiosoma of the specimen figured measures 1575 μm long × 1110 μm wide. It is entirely reticulated, with a transverse median suture (Fig. 42H). The podonotal setae are largely pilose to some degree, setae *z5* (190 μm long) and *r3* (300 μm long) are the stoutest. The setae of the opisthonotal region are mainly homogeneous, being curved and finely pilose (see inset to figure 42H). The tritosternum has a narrow base and pilose laciniae. The genital lamina protrudes from beneath the sternogenital shield. Sternal setae I–III narrow successively and, with setae IV, are finely pilose. The reticulated holoventral shield retains some of the deutosternal striations (Fig. 42I). The opisthogastric setae are fine and pointed. The postanal seta is approximately three times as long as the paranal setae and is stouter. Small circular granular areas are located at the approximate positions of the metapodal shields of the deutonymph. The peritreme extends to the level of coxa I.

The tectum is of irregular outline (Fig. 42J). The chelicera is shown in figure 42K, and the chaetotaxy of the palp trochanter, femur and genu in figure 42L. The corniculi are cleft on the inner margins and the gnathosomal setae are as in figure 42M. The chaetotaxy and armature of leg II are shown in figure 42N. The setae of leg I are strong but slender, many

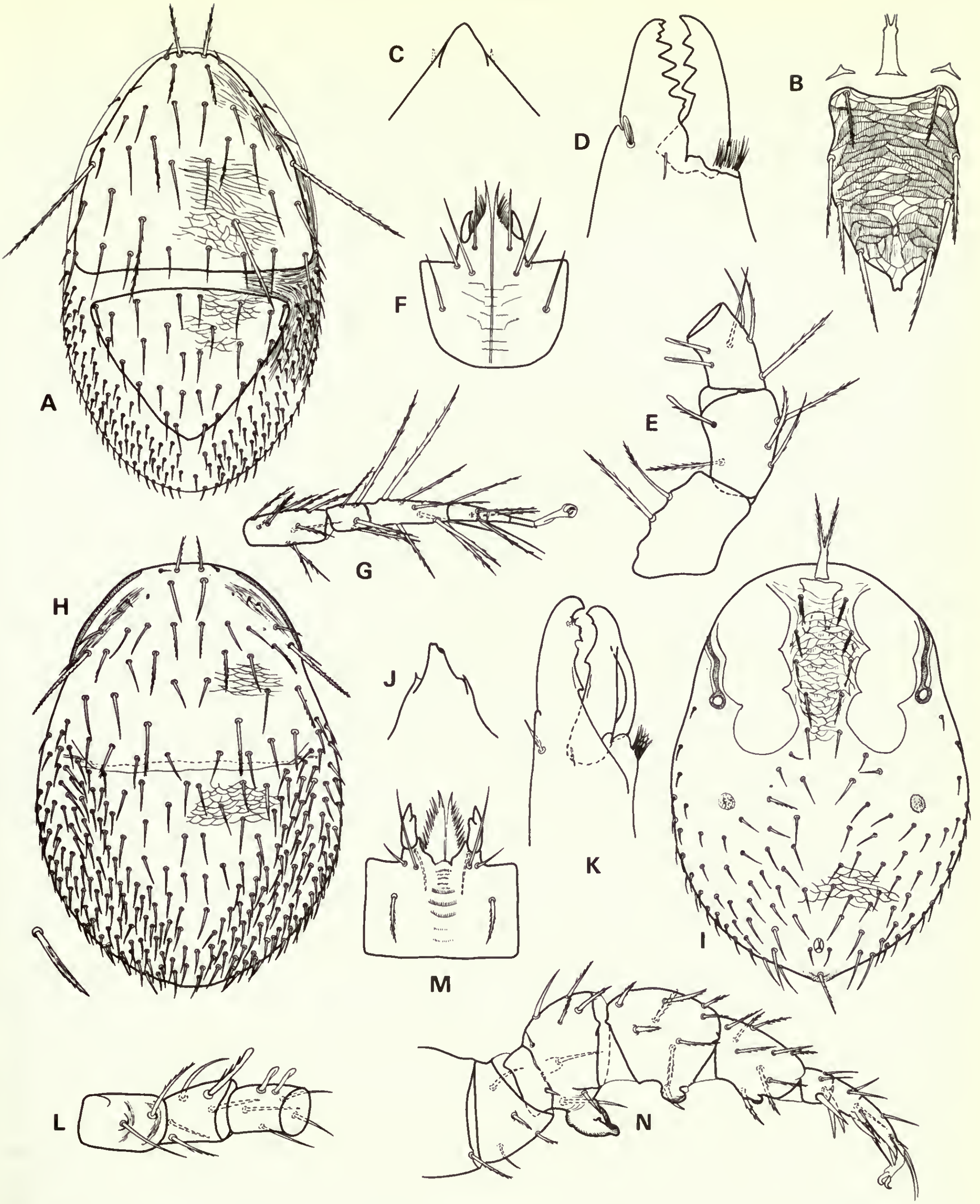


Fig. 42 *Parasitellus fucorum* (De Geer), **deutonymph** – A dorsum; B sternal shield; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma; G tarsus IV: **male** – H dorsum; I venter; J tectum; K chelicera; L palp trochanter, femur and genu; M venter of gnathosoma; N leg II.

having fine pilosity. Leg III has mainly strong curved setae with the genu and tibia each bearing a pair of stout ventral setae, whilst the tarsus bears stouter setae ventrally and laterally. The setae of leg IV are stouter towards the tibia and tarsus.

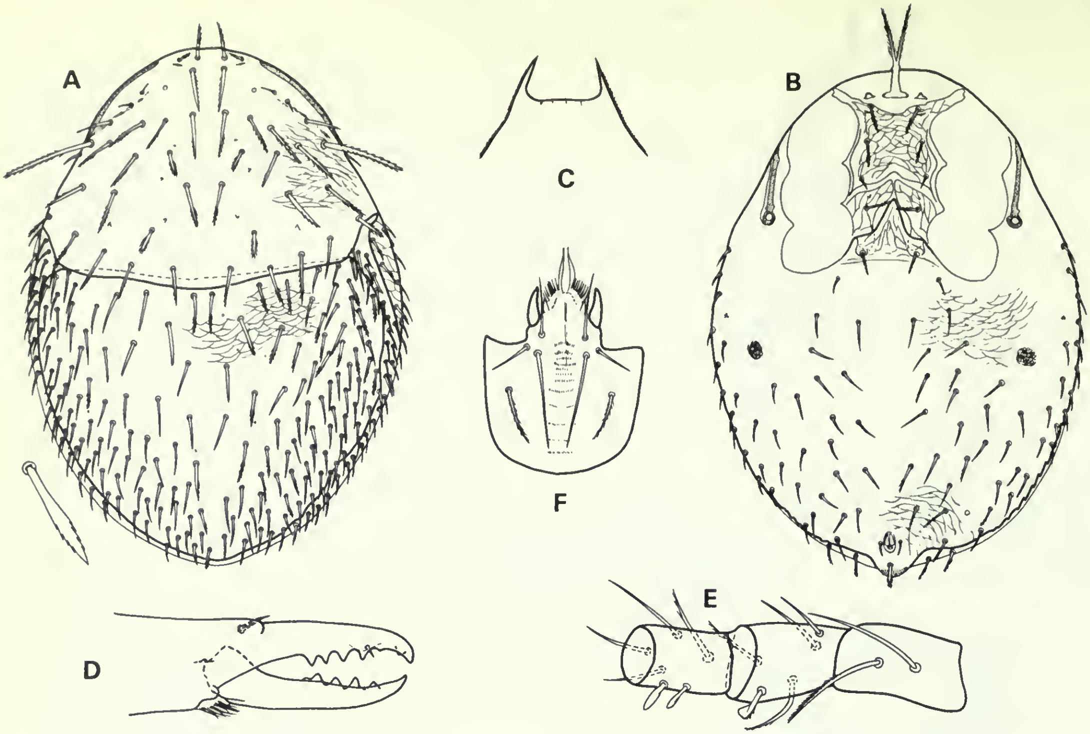


Fig. 43 *Parasitellus fucorum* (De Geer), **female** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma.

FEMALE. The idiosoma of the specimen figured measures 1680 µm long × 1140 µm wide, the podonotal shield being *c.* 790 µm long and the opisthonotal *c.* 950 µm, there being a small overlap. The podonotal shield is fused with the ventral sclerotization which extends to the dorsal surface at the widest point (Fig. 43A). The opisthonotal shield occupies almost the full width of the posterior region, being surrounded by a narrow area of membrane. The dorsal chaetotaxy differs from that of the male in that *j4* and *z5* are both considerably shorter (*c.* 60–70 µm) than their adjacent setae, and all the setae are generally stouter (see inset to figure). Setae *r3* are *c.* 300 µm.

The tritosternum has a narrow base with a rather broader than usual 'foot' and has pilose laciniae. The presternal shields are small (Fig. 43B). The sternal, metasternal and genital shields are well sclerotized and reticulated and the setae are finely pilose. The opisthogastric region is entirely reticulated and the setae are mainly curved, with very fine pilosity. The paranal setae are short and the postanal is slightly longer, stouter and pilose. As in the male, circular granular areas are present at the metapodal positions. The peritreme extends to coxa I.

The tectum is quite unlike either the deutonymph or male. It comprises two widely spaced but converging slender tines, each finely denticulate on the outer margin (Fig. 43C). The cheliceral teeth are well developed and the digits are slender (Fig. 43D). The chaetotaxy of the palp trochanter, femur and genu is shown in figure 43E. The venter of the gnathosoma is as in figure 43F, the internal posterior hypostomatic setae being the longest. The setae on leg I are mainly fine and slender, but on legs II–IV they are considerably stouter and are largely pilose.

MATERIAL EXAMINED. 123 samples – 1180+DNN, 30 ♂♂, 39 ♀♀, plus three samples containing respectively 130, 170 and 275 deutonymphs of which a proportion were examined closely.

ENGLAND: Cornwall, Isles of Scilly, Devon, Somerset, Dorset, Gloucestershire, Hampshire, Surrey, Kent, Essex, London, Middlesex, Berkshire, Hertfordshire, Buckinghamshire, Oxfordshire, Norfolk, Huntingdonshire, Nottinghamshire, Derbyshire, Cheshire, Manchester, Lancashire, Cumberland, Northumberland, Yorkshire.
WALES: Caernarvonshire, Denbighshire.
SCOTLAND: Fifeshire, Orkney, Fair Isle, Shetland, Arran
IRELAND: Galway.
CHANNEL ISLANDS: Guernsey.

This common European species is almost certainly distributed throughout the British Isles. With few exceptions all the material examined is from *Bombus* spp. The exceptions are 12 samples from *Psithyrus* spp., three deutonymphs from *Otiorhynchus sulcatus* (Fabricius) (Coleoptera, Curculionidae) (the only Irish material examined), one deutonymph from *Chrysis ignita* (L.) (Hymenoptera, Chrysididae) from Berkshire, five samples from flowers, presumably visited by *Bombus,* and one sample of 26 deutonymphs on *Juniperus* sp. in Kent. Four of the total samples examined have no habitat data.

DISTRIBUTION. Surprisingly the only previous British records for this well-known species are from the Tyne Province (Hull, 1917 – *bombianus* and *nidicolens,* and Hull, 1918 – *fucarius*) and from Guernsey (Le Pelley, 1972). The specimens examined by Colombo (1961) from Surrey, Middlesex and Berkshire, have so far not been recorded. The inclusion by Micherdzinski (1969) of this species being recorded by Turk & Turk (1952) is erroneus. The records of *Parasitus bomborum* Oudemans, 1902*b*, by Stebbing (1965*a*, 1965*b*) cannot be taken as correct identifications and these specimens are not now available for examination (Stebbing, pers. comm.). Subsequent specimens collected by Stebbing from bumblebees in Essex, Hertfordshire and Huntingdonshire in 1969 represent all four species of *Parasitellus* and are incorporated into the relevant species records.

It is recorded from Swedish Lapland (Trägårdh, 1910), Holland (Oudemans, 1902*b,* 1906), France (Berlese, 1906, Schmölzer, 1956), Germany (Voigts & Oudemans, 1905, Willmann, 1939*b,* Karg, 1965, 1971, Holzmann, 1969), Switzerland (Schweizer, 1949, 1961), Italy (Berlese, 1906), Poland (Micherdzinski, 1969, Chmielewski, 1971), Greece (Oudemans, 1905*b*) and Western Siberia (Davydova, 1976).

Parasitellus crinitus (Oudemans) comb. nov.
(Figs 44 A–M; 45A–F)

Parasitus crinitus Oudemans, 1903*b*: 85; 1905*a*: 79. Berlese, 1906: 264. (Non Vitzthum, 1930*a*: 31 = *P. ignotus* Vitzthum, 1930*a*).
Parasitus crinitosimilis Vitzthum, 1930*a*: 33 (DN). Colombo, 1961. Micherdzinski, 1969: 608. (Non Holzmann, 1969: 55 = *P. talparum* (Oudemans, 1913*a*). Karg, 1971: 451. **Syn. nov.**
Parasitus (Parasitus) crinitosimilis: Tichomirov, 1969: 1476. Bregetova *et al.,* 1977: 74.
Parasitus dubiosus Vitzthum, 1930*a*: 37 (♀). Colombo, 1961. Micherdzinski, 1969: 601. Karg, 1971: 450. **Syn. nov.**
Parasitus (Parasitus) dubiosus: Tichomirov, 1969: 1476. Bregetova *et al.,* 1977: 74.
Parasitus talparum Oudemans, 1913*a* sensu Lundqvist & Micherdzinski, 1975: 71 (♀ only).

DEUTONYMPH. The podonotal shield averages 400 μm long × 430 μm wide, is entirely reticulated and bears 21 pairs of setae, several of which are sparsely pilose (Fig. 44A). The majority are long and the longest, *r3* and *z5,* measure *c.* 230 μm and *c.* 180 μm respectively. The opisthonotal shield averages 252 μm long × 372 μm wide and bears up to about 40 pairs of slender simple setae, mainly arranged symmetrically, but with additional unpaired setae amongst the *J*-series.

The tritosternum, which has a narrow base and pilose laciniae, is flanked by a pair of small but conspicuous presternal shields (Fig. 44B). The sternal shield averages 275 μm long, is strongly reticulated and the four pairs of setae are long and slender, with *st.* I and II bearing sparse pilosity. The opisthogastric setae are fairly dense, several may be fused onto the edge of the ovoid reticulated anal shield. The paranal setae are shorter than the postanal and all three are more slender than the opisthogastric setae. The peritreme extends to coxa I.

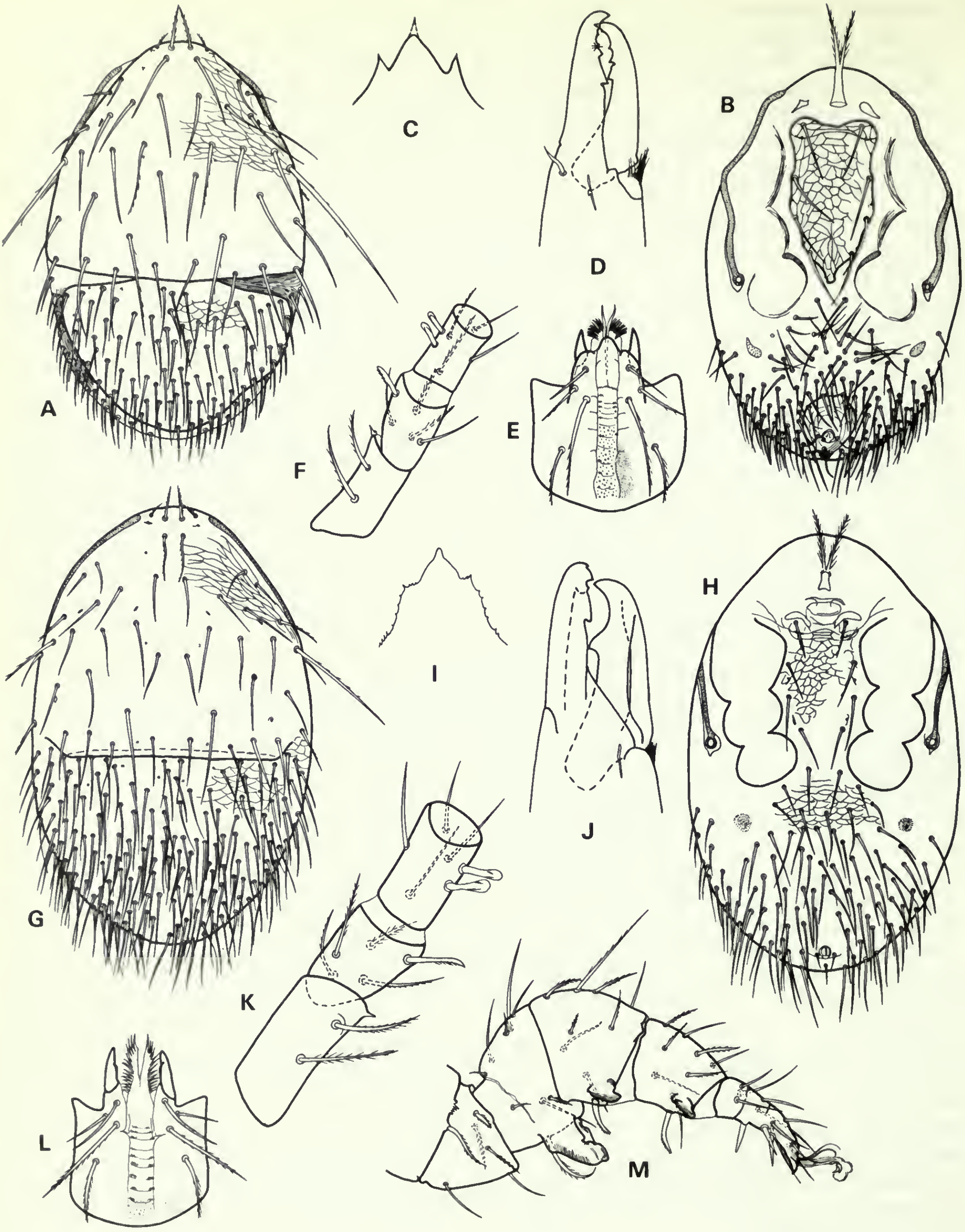


Fig. 44 *Parasitellus crinitus* (Oudemans), **deutonymph** – A dorsum; B venter; C tectum; D chelicera; E venter of gnathosoma; F palp trochanter, femur and genu: **male** – G dorsum; H venter; I tectum; J chelicera; K palp trochanter, femur and genu; L venter of gnathosoma; M leg II.

The tectum is trispinate: the centre portion is broad and tapers to a fine short point which may be broken off, whilst the two lateral spines are smaller and pointed (Fig. 44C). The chelicera is shown in figure 44D, the venter of the gnathosoma in figure 44E, and the palp trochanter, femur and genu in figure 44F. The setae on legs I and II are the finest and some are pilose; leg III bears stouter pilose setae, especially on the tarsus, and leg IV bears two long setae dorsally on the tarsus which measure *c.* 125 μm and *c.* 175 μm respectively.

MALE. The idiosoma (940–960 μm long × 550–635 μm wide) is strongly sclerotized and entirely reticulated (Fig. 44G). The podonotal region bears 23 pairs of setae of which the longest are *z5* (210 μm) and *r3* (275 μm). The opisthonotal setae are numerous and evenly distributed.

The tritosternum has a short, narrow, base and pilose laciniae. The presternal shields appear to be engulfed by the anterior reaches of the sternal sclerotization and the genital lamina is not very conspicuous (Fig. 44H). The holoventral shield is strongly reticulated. The sternal setae are slightly stouter than the longer opisthogastric setae and may be sparsely pilose. The three anal setae are shorter and subequal in length. The peritreme extends to coxa I.

The tectum comprises a broad tapered central region with serrated posterior margins (Fig. 44I). The chelicera is shown in figure 44J, the fixed digit extends slightly beyond the tip of the movable. The chaetotaxy of the palp trochanter, femur and genu is as in figure 44K, and the venter of the gnathosoma in figure 44L. The inner margins of the corniculi are slightly stepped. Leg II is shown in detail in figure 44M. Leg I bears mainly fine setae, but the trochanter and femur each bear dorsally one short stout seta and a second seta slightly less stout. Legs III and IV bear stouter setae, especially on the tibia and tarsus.

FEMALE. The podonotal shield measures, in the single specimen examined, 540 μm long × 570 μm wide. It is lightly reticulated in the anterior and lateral portions, and is finely granular all over (Fig. 45A). It bears 21 pairs of setae of which some show sparse pilosity. Only *z5* (*c.* 185 μm) and *r3* (*c.* 220 μm) are long. The opisthonotal shield is granular and entirely reticulated. It measures 490 μm long × 530 μm wide and bears about 45–50 pairs of fine slender setae. The posterior membrane bears similar setae.

The tritosternum is flanked by a pair of inconspicuous but granular presternal shields (Fig. 45B). The ventral shields are all granular and strongly reticulated. The sternal setae are the stoutest and, like the genitals, are finely pilose. The metasternal and opisthogastric setae are probably all simple, although about half the opisthogastrics, which are not entirely symmetrical in their arrangement, are missing. The postanal seta is slightly longer than the paranals. The peritreme extends to coxa I.

The tectum is shown in figure 45C: the centre prong is slightly divided at its tip and the lateral teeth are not symmetrical. The chelicera is as in figure 45D: the fixed digit bears minute teeth between the tip and the first main tooth. The chaetotaxy of the palp trochanter, femur and genu is shown in figure 45E, and the venter of the gnathosoma in figure 45F. All legs bear mainly simple setae, those on leg I being the most slender. Leg II bears a stout ventral seta on the tarsus and tibia, plus two short downcurved distal spurs on the tarsus. Several setae are missing from both legs IV, but I believe no long setae are normally present on the tarsus.

MATERIAL EXAMINED. 8 samples – 9DNN, 2 ♂♂, 1 ♀.

ENGLAND: Surrey, London, Buckinghamshire, Norfolk, Huntingdonshire, Derbyshire and Lancashire.

All material was associated with *Bombus* spp. or their nests, with the exception of a single deutonymph from Wimbledon Common, southwest London, that was collected on a shrew *Sorex* sp.

DISTRIBUTION. Colombo (1961) examined specimens from Surrey, Middlesex and Buckinghamshire but these records have remained unpublished. Therefore *Parasitellus*

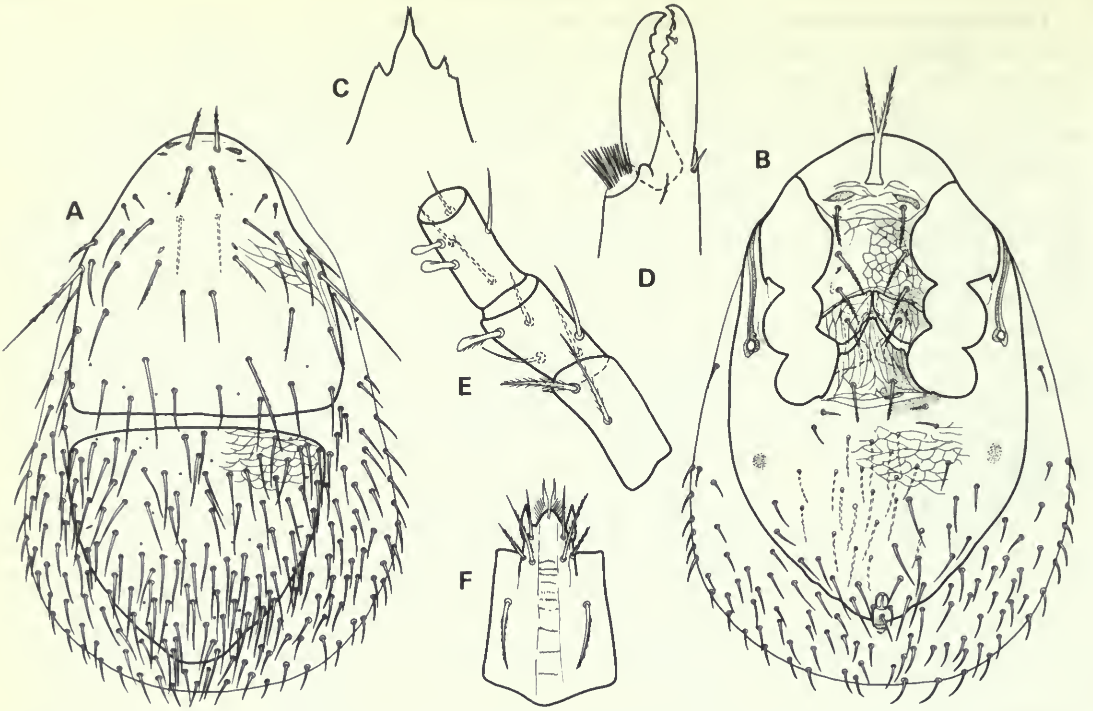


Fig. 45 *Parasitellus crinitus* (Oudemans), **female** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma.

crinitus is now recorded for the first time from the British Isles. Additionally it is only authentically recorded from Germany (Oudemans, 1905*a*, Willmann, 1939*b*, Vitzthum, 1930*a*).

Parasitellus ignotus (Vitzthum) comb. nov.
(Figs 46A–M; 47A–F)

Parasitus ignotus Vitzthum, 1930*a*: 40 (♀). Colombo, 1961. Micherdzinski, 1969: 531. Karg, 1971: 449.

Parasitus (Parasitus) ignotus: Tichomirov, 1969: 1476. Bregetova *et al.*, 1977: 72.

Parasitus crinitus Oudemans, 1903*b* sensu Vitzthum, 1930*a*: 31 (DN). Colombo, 1961. Micherdzinski, 1969: 608. Holzmann, 1969: 55. Karg, 1971: 451.

DEUTONYMPH. The podonotal shield (396–415 μm long × 384–520 μm wide) is well sclerotized and entirely reticulated (Fig. 46A). It bears 22 pairs of setae, most of which are rather long (*r3* are *c.* 205 μm) and well surpass the bases of the next posterior one. Some are finely pilose. The fine and slender *s1* and *s2* can be either on or off the shield and are included here as being on. An additional seta is located between *r5* and *s6.* The triangular opisthonotal shield (up to 280 μm long × 390 μm wide) is also entirely reticulated. It bears over 30 pairs of setae, those in the posterolateral region being shorter and more closely spaced than those situated medially. Additionally a cluster of up to five or six short setae are situated between *J1* and *J3.* The setae on the posterior interscutal membrane are numerous and appear as a continuation of those in the posterolateral area of the shield.

The tritosternum, which has a narrow base and pilose laciniae, is flanked by a pair of small rather irregularly shaped presternal shields (Fig. 46B). The sternal shield (280–336 μm long) is entirely reticulated, but the area anterior to the first pair of pores is weakly sclerotized. The setae are long and slender. The opisthogastric region is densely pilose, the setae range from about 40–50 μm in length. The anal shield is subcircular to oval and is reticulated. The

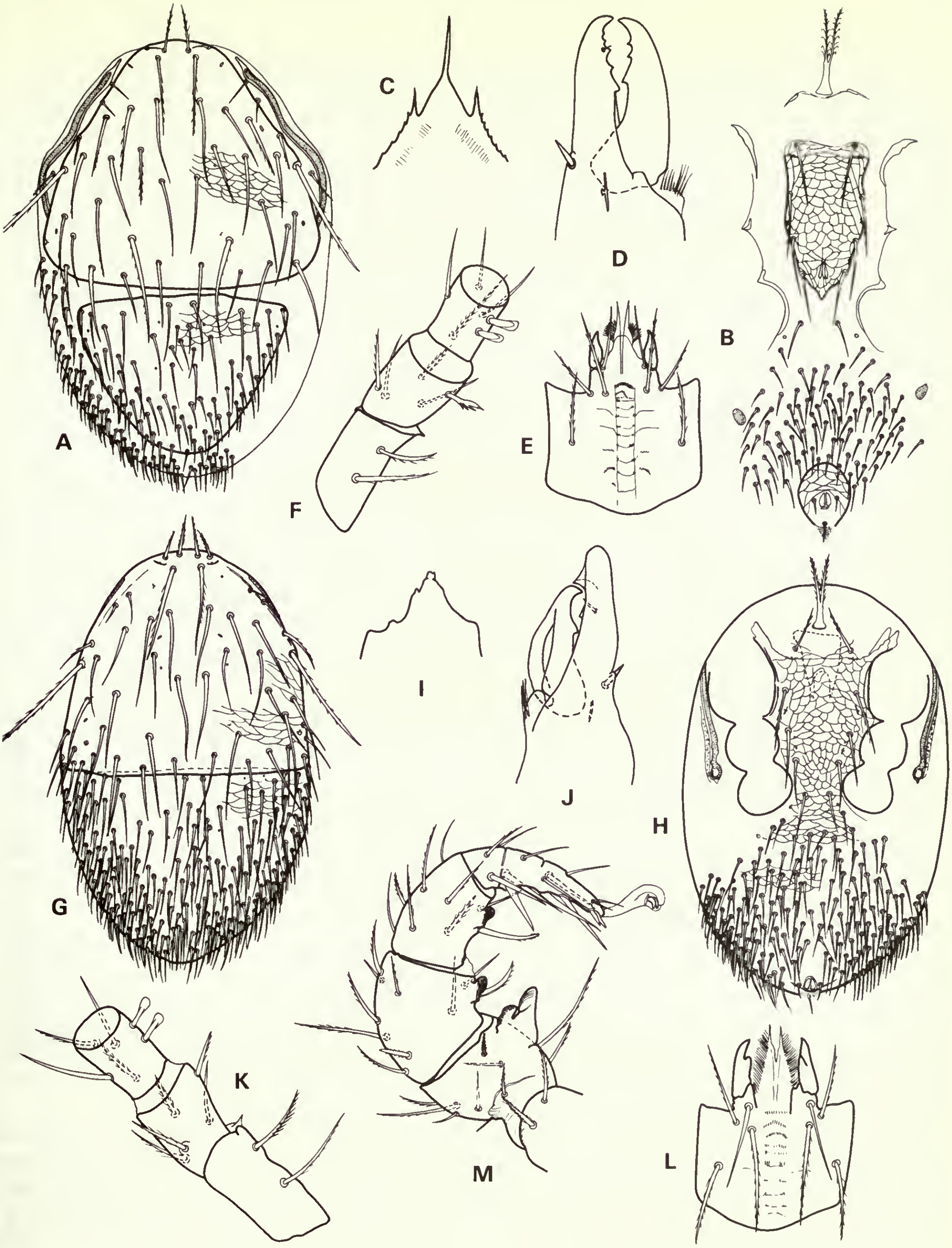


Fig. 46 *Parasitellus ignotus* (Vitzthum), **deutonymph** – A dorsum; B venter; C tectum; D chelicera; E venter of gnathosoma; F palp trochanter, femur and genu: **male** – G dorsum; H venter; I tectum; J chelicera; K palp trochanter, femur and genu; L venter of gnathosoma; M leg II.

postanal seta is slightly stouter and longer than the paranals. The peritreme extends to coxa I.

The tectum is trispinate (Fig. 46C). The centre prong has a broad base and tapers narrowly, the lateral spines are short and sharp with their basal edges toothed. The chelicera is shown in figure 46D, the venter of the gnathosoma in figure 46E, and the chaetotaxy of the palp trochanter, femur and genu in figure 46F. The setae on legs I and II are the finest and many are pilose. Leg III bears generally stouter setae which are almost all pilose, and dorsally on the femur is a conspicuous pilose seta distally. Leg IV has similar setae to leg III, but in addition the tarsus bears dorsally two conspicuously long setae measuring *c.* 240 μm and 300 μm.

MALE. The idiosoma averages 865–925 μm long × 480–540 μm wide and is entirely reticulated and with a transverse suture (Fig. 46G). The podonotal setae are mainly long and often sinuous with *r3* the longest (*c.* 200 μm). Most are finely pilose, but *s1* and *s2* are the shortest (*c.* 35 μm) and are very slender. The opisthonotal setae are numerous and densest in the posterolateral area where they are considerably shorter than those situated medially.

The tritosternum is present, but the presternal shields are absent. The holoventral region is well sclerotized and heavily reticulated (Fig. 46H). The sternogenital setae are the longest and the opisthogastric setae are dense. The postanal seta is slightly longer than the paranals and the peritreme extends to coxa I.

The tectum is presumably rarely of symmetrical appearance and a 'typical' example is shown in figure 46I. The fixed digit of the chelicera extends beyond a large terminal tooth below which the movable digit (98 μm) fits closely (Fig. 46J). The chaetotaxy of the palp trochanter, femur and genu is shown in figure 46K, and the venter of the gnathosoma in figure 46L. The corniculi are slender, notched internally and with the tips curved inwards. Leg II is shown in detail in figure 46M. The setae of leg I are mainly fine and simple. Tibiae III and IV each bear an erect seta dorsally and tarsus IV has two long dorsal setae measuring *c.* 212 μm and 237 μm.

FEMALE. The reticulated podonotal shield averages 505 μm long × 610 μm wide and is attenuated posterior to setae *r3* (Fig. 47A). It bears 23 pairs of setae, several of which are finely pilose. Setae *r3* are the longest (*c.* 250 μm) whilst *s1, s2* and *r4* are situated on the shield. The opisthonotal shield averages 515 μm long × 490 μm wide and fits closely against the podonotal. It bears about 50 pairs of rather long simple setae all of which surpass the bases of at least one succeeding seta. In some specimens a narrow strip of the interscutal membrane is sclerotized where it abuts the posterior region of the opisthonotal shield. This feature may also be encountered in the females of *P. talparum* (p. 337).

The tritosternum is flanked by a pair of small inconspicuous presternal shields (Fig. 47B). The sternal shield is heavily reticulated with an area of coarse granulation between setae III and the edge of the shield. Sternal setae I and II are slightly stouter than III, IV and the genital setae, and are more clearly slightly pilose. The genital shield is rounded, tapered anteriorly, and a small pair of conspicuous horns are situated laterally. The opisthogastric region is strongly reticulated and bears about 35 pairs of simple setae similar to the genital setae. The paranal setae are approximately half the length of the postanal. The opisthogastric shield is also bordered by a strip of sclerotized membrane. The peritreme extends to coxa I.

The tectum (Fig. 47C) is similar to that of the deutonymph. The chelicera is shown in figure 47D, the chaetotaxy of the palp trochanter, femur and genu in figure 47E, and the venter of the gnathosoma in figure 47F. The anterior hypostomatic setae appear to be the only pair that is simple. The corniculi are slightly undulating on their inner margins. All legs bear mainly pilose setae, those on leg I being the most slender. Tarsus IV bears two erect dorsal setae up to 250 μm in length.

MATERIAL EXAMINED. 11 samples – 24 DNN, 4 ♂♂, 6 ♀♀.

ENGLAND: Surrey, Essex, Hertfordshire, Berkshire, Norfolk, Huntingdonshire and Lancashire.

IRELAND: Cork.

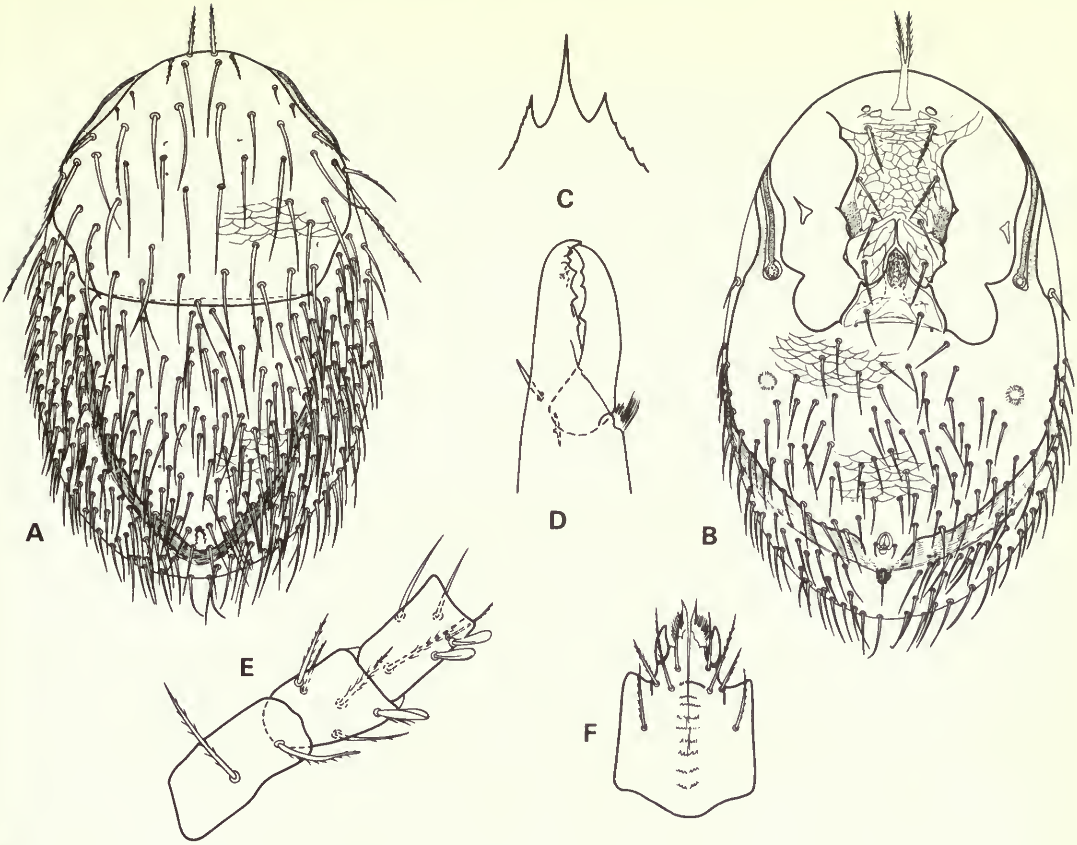


Fig. 47 *Parasitellus ignotus* (Vitzthum), **female** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma.

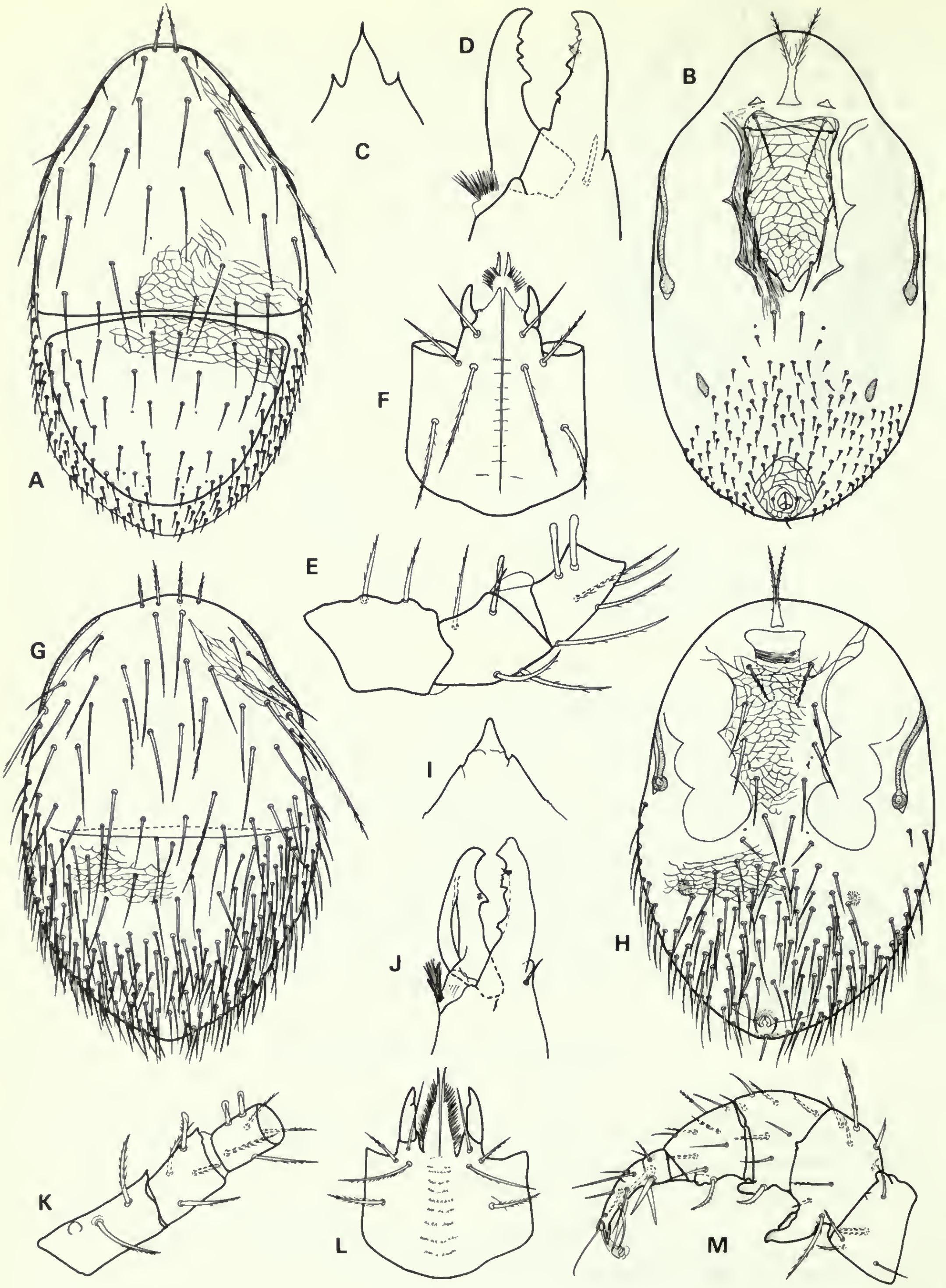
Ten of the samples were associated with *Bombus* spp. and their nests. The exception was five deutonymphs and three males from a nest of starling *Sturnus vulgaris* L. in the burrow of a sand martin *Riparia riparia* (L.) in Co. Cork, 3 June 1964. It is more than likely that bumblebees were also associated with the burrow.

DISTRIBUTION. Since Vitzthum's original description of presumably German material was published in 1930, the only other authentic record of this species appears to be that of Colombo (1961) who collected material in Surrey, Middlesex and Buckinghamshire. However, as these records are unpublished *Parasitellus ignotus* is now recorded for the first time from the British Isles.

Parasitellus talparum (Oudemans) comb. nov.

(Figs 48A–M; 49A–F)

Parasitus talparum Oudemans, 1913*a*: 333; 1914, Heft 8: 108. Turk & Turk, 1952: 477. Turk, 1953: 10. Micherdzinski, 1969: 605. Karg, 1971: 450. Lundqvist & Micherdzinski, 1975: 71 (DN only). Type examined.
Parasitus (Parasitus) talparum: Tichomirov, 1969: 1476.
Parasitus bombophilus Vitzthum, 1930*a*: 25 (DN, ♂). Karg, 1971: 449. Davydova, 1976: 61. **Syn. nov.**
Parasitus (Parasitus) bombophilus: Tichomirov, 1969: 1476.
Parasitus traegardhi Micherdzinski, 1969: 567. Karg, 1971: 449.
Parasitus (Parasitus) tragardhi: Bregetova *et al.*, 1977: 74 (lapsus pro *traegardhi*).
Parasitus bomborum Oudemans sensu Trägårdh, 1904: 35.
Parasitus fucorum (De Geer) sensu Trägårdh, 1910: 384.


A
B
C
D
E
F
G
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K
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M

Parasitus anglicus Vitzthum, 1930*a*: 35 (DN). Micherdzinski, 1969: 608 (non *Gamasus anglicus* Hull, 1918 = *Parasitus loricatus* (Wankel)). **Syn. nov.**

Parasitus numismaticus Vitzthum, 1930*a*: 42 (♀). Colombo, 1961. Micherdzinski, 1969: 433. Davydova, 1969: 23, 24, 26; 1976: 58. Holzmann, 1969: 55. Karg, 1971: 449. **Syn. nov.**

Parasitus (Parasitus) numismaticus: Tichomirov, 1969: 1476. Bregetova *et al.*, 1977: 72, 74.

Davydova (1976) records both *P. numismaticus* and *P. bombophilus.* Her figures labelled *numismaticus* (DN, ♂, ♀) are typical of the range I have encountered in *talparum,* whilst those labelled *bombophilus* (♂, ♀), although bearing rather short idiosomal setae, are still within the range.

DEUTONYMPH. The podonotal shield (420–525 μm long × 420–540 μm wide) is entirely reticulated and bears 21 pairs of setae, the longest being *z5* (*c.* 220 μm) and *r3* (*c.* 270 μm), the latter being sparsely pilose (Fig. 48A). Setae *j1* and *j2* are also usually pilose. The fine slender setae *s1* and *s2* can be either on or off the shield and are included here as being on. The opisthonotal shield (276–360 μm long × 360–480 μm wide) is also reticulated. It bears from 24 to 30 pairs of setae which are not always located symmetrically around the posterolateral margins. Anteriorly the setae are of similar length to the shorter podonotals, but posteriorly they resemble the dense interscutal setae which themselves become shorter posteriorly, ranging from 45–20 μm.

The tritosternum has a narrow base and pilose laciniae. It is flanked by small triangular presternal shields. The sternal shield (Fig. 48B) is clearly reticulated and measures 300–350 μm in length. The portion anterior to sternal pores I is often lighter coloured than the remainder. The setae are long and slender with fine pilosity on I and II. The reticulated anal shield is broadly oval, the three anal setae are of approximately equal length. The dense opisthogastric setae are longest anteriorly (*c.* 30 μm), becoming short posteriorly (*c.* 13 μm minimum). The metapodal shields are granular and the peritreme extends anteriorly to coxa I.

The tectum normally comprises a broad tapered tongue flanked by a pair of pointed teeth (Fig. 48C), but irregularities occur. The chelicera is shown in figure 48D. The chaetotaxy of the palp trochanter, femur and genu is as in figure 48E, and the venter of the gnathosoma in figure 48F. The corniculi are smoothly pointed and the internal posterior hypostomatic setae are the longest. The setae of leg I are slender. Leg II bears stout ventral setae on the tibia and tarsus. On legs III and IV the setae are generally stouter, especially on tibia and tarsus IV, whilst tarsus IV bears additionally two long dorsal setae (*c.* 370 μm) similar to *Parasitellus fucorum.*

MALE. The idiosoma measures 1150–1260 μm long × 780–840 μm wide. It is entirely reticulated and with a transverse suture (Fig. 48G). The majority of the setae are long, very slender and, apart from a few sparsely pilose pairs in the podonotal region, all are simple. Setae *z5* (*c.* 280 μm) and *r3* (330 μm) are the longest.

The tritosternum has a short narrow base and pilose laciniae. The genital lamina often protrudes from the sternogenital shield (Fig. 48H). The holoventral shield is reticulated. The slender sternal setae bear traces of pilosity, whereas the rather numerous opisthogastric setae are simple. Faint circular granular areas are present at the equivalent location of the metapodal shields of the deutonymph. The postanal seta is almost one and a half times as long as the paranals and is stouter. The peritreme extends to the level of coxa I.

The tectum is rather irregular in outline, but it comprises a triangular tongue with a pair of small lateral prongs (Fig. 48I). The chelicera is shown in figure 48J and the chaetotaxy of the palp trochanter, genu and tibia in figure 48K. The corniculi are slender, finely cleft on their inner margins, and the internal posterior hypostomatic setae are the longest (Fig. 48L). The chaetotaxy and armature of leg II are shown in figure 48M. The trochanter bears a small

Fig. 48 *Parasitellus talparum* (Oudemans), **deutonymph** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma: **male** – G dorsum; H venter; I tectum; J chelicera; K palp trochanter, femur and genu; L venter of gnathosoma; M leg II.

conspicuous anteriorly directed domed or pointed spur dorsally. The setae on leg I are the most slender, many are finely pilose. Legs III and IV have stouter setae and tarsus IV bears two long dorsal setae (*c.* 359 μm) as in the deutonymph.

FEMALE. The podonotal shield measures 720 μm long × 780 μm wide. It is entirely reticulated and bears 23 pairs of setae (Fig. 49A), most of which are finely pilose to a certain extent with *z5* and *r3* the longest. The opisthonotal shield measures 720 μm long × 756 μm wide and is entirely reticulated. Occasionally a sclerotized strip of cuticle borders the shield, a feature which is frequently encountered in the Macrochelidae, but only rarely in other gamasines. About 40 pairs of setae are present, those anteriorly being the longest and resembling those of the podonotal shield, whilst posteriorly they become progressively shorter to about 30 μm. The surrounding membrane is well clothed with setae laterally, becoming more sparse posteriorly.

The tritosternum has a narrow base and pilose laciniae. The presternal shields are coalesced to form a narrow strip (Fig. 49B). The sternal shield is strongly reticulated posterior to pore I, whilst adjacent to setae III lies a pair of circular granular areas. The metasternal and genital shields are weakly reticulated. The sternogenital setae are strongly formed and finely pilose. The opisthogastric shield is finely reticulated except for an area posterior to coxae IV which is ornamented with heavy crenate reticulations. In some specimens the posterior margin is bordered by a sclerotized strip of cuticle. About sixteen setae in the centre of the opisthogastric shield are conspicuously long and finely pilose, whereas the remainder are short and fine. The paranal setae are also short and fine, but the postanal is longer, stouter and pilose. As in the male, circular granular areas are present at the metapodal positions. The peritreme extends to coxa I.

The tectum is shown in figure 49C, the chelicera in figure 49D, the chaetotaxy of the palp trochanter, femur and genu in figure 49E, and the venter of the gnathosoma in figure 49F: the internal posterior hypostomatic setae are the longest. The setae on leg I are mainly fine and slender. On leg II the genu, tibia and tarsus each bear a single stout seta ventrally. Leg III bears ventrally on the genu and tibia a pair of stout setae and on the tarsus a single one. Leg IV bears generally stouter setae, especially on the tibia and tarsus.

MATERIAL EXAMINED. 30 samples – 83 DNN, 16 ♂♂, 16 ♀♀.
ENGLAND: Devon, Hampshire, Gloucestershire, Oxfordshire, Berkshire, Middlesex, Essex, Norfolk, Huntingdonshire, Lancashire, Cheshire.
SCOTLAND: Edinburgh district, Outer Hebrides (Isle of Lewis).
IRELAND: Dublin.

Most of the material examined is from bumblebees of the genus *Bombus,* but two single deutonymphs are from *Apodemus sylvaticus* (L.) and two are from flower-heads.

DISTRIBUTION. The only previous records of this species from the British Isles are by Vitzthum (1930*a*) who described *Parasitus anglicus* from two deutonymphs collected by O. W. Richards on *Bombus lapidarius* (L.) at Oxford. Turk & Turk (1952) identified two deutonymphs from the nest of *Apodemus sylvaticus* (L.) at North Bull, Dublin as *Parasitus talparum* Oudemans. I have examined one of the Dublin specimens and agree with the designation. Colombo (1961) examined *numismaticus* from Surrey, Middlesex and Buckinghamshire, but these records have until now remained unpublished.

This species is recorded from Greenland (Trägårdh, 1904), Swedish Lapland (Trägårdh, 1910), southern Sweden (Lundqvist, 1974, Lundqvist & Micherdzinski, 1975), Germany (Vitzthum, 1930*a*), Holland (Oudemans, 1913*a*, 1914), Switzerland (Schweizer, 1949, 1961), Czechoslovakia (Micherdzinski, 1969) and Western Siberia (Davydova, 1969, 1976).

Genus ***GAMASODES*** Oudemans

Gamasodes Oudemans, 1939. *Zool. Anz.* **126**: 24.

TYPE SPECIES. *Gamasoides spiniger* Oudemans, 1936 (= *Eugamasus spiniger* Trägårdh, 1910).

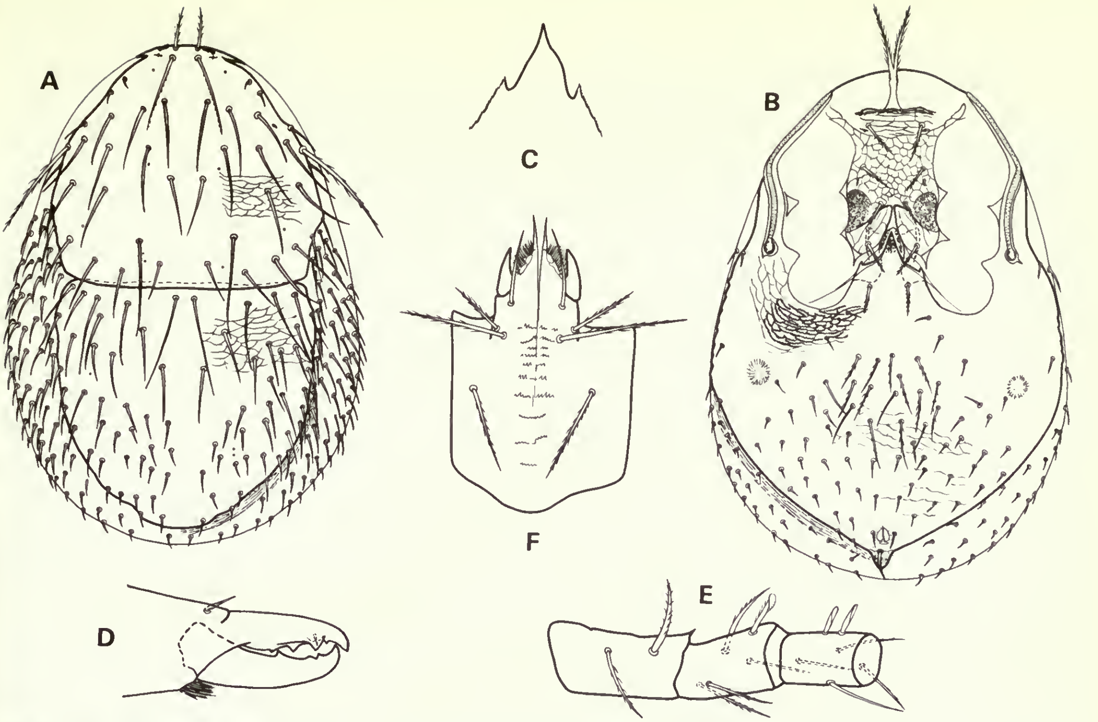

Fig. 49 *Parasitellus talparum* (Oudemans), **female** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma.

Dorsal shield of male entire, with transverse suture; female and deutonymph with separate podonotal and opisthonotal shields, or female with schizodorsal shield. Setae *z5* of dorsal hexagon differing in length and form from setae *j5* and *j6*, or if similar, then female with schizodorsal shield. Tritosternum of male absent or rudimentary, that of deutonymph and female normal, biramous. Junction between sternal and metasternal shields of female oblique. Genital shield of female subtriangular. Opisthogaster with rarely more than 18 pairs of setae. Seta *al* of palp femur setiform, with or without spicules; setae al_1 and al_2 of palp genu spatulate. Male chelicerae symmetrical. Corniculi entire, short, tapered. Leg II of deutonymph with strong slender spurs; leg II of female sometimes with spurs or modified setae; leg II of male spurred. Lobes of pulvilli normal, rounded.

Gamasodes spiniger (Trägårdh)
(Figs 50A–N; 51A–G)

Gamasus spinipes C. L. Koch, 1844, non Say, 1821, teste Oudemans, 1936: 202.
Poecilochirus spinipes: Berlese, 1892*b*: Fasc. 69, T. 4.
Gamasoides spinipes: Halbert, 1915: 55; 1920: 119, in part. Oudemans, 1939*a*: 24.
Gamasoides spiniger Oudemans, 1936: 202, *nom. nov. pro Gamasus spinipes* Koch.
Gamasodes spiniger Oudemans, 1936. Oudemans, 1939*b*: 199. Strenzke, 1951: 20. Schweizer, 1961: 11.
Eugamasus spiniger Trägårdh, 1910: 402.
Gamosodes spiniger (Trägårdh, 1910). Costa, 1961: 271. Micherdzinski, 1969: 616. Karg, 1971: 416. Bregetova *et al.*, 1977: 94, 95. Evans & Till, 1979: 210.
Parasitus lunarisimilis Schweizer, 1961: 18. Micherdzinski, 1969: 550. Karg, 1971: 447. **Syn. nov.** Type examined.

DEUTONYMPH. The podonotal shield (312–348 μm long × 372–420 μm wide) is strongly sclerotized and entirely reticulated. It bears 19 pairs of setae of which *j1* and *r3* are the stoutest, longest and are pilose. The remaining setae are mainly finely pointed and simple, although sparse pilosity does occur on a few. Setae *s2* and *r2* are situated off the shield (Fig. 50A). The opisthonotal shield (204–240 μm long × 324–384 μm wide) is of similar structure to the podonotal and bears 14 pairs of setae of which three pairs, *J5, Z1* and *Z3* are generally stouter, longer, and pilose. As on the podonotal shield, other setae may possess sparse pilosity.

The tritosternum has a narrow base and pilose laciniae. It is situated slightly anterior to the presternal shields which are broad and almost meet medially. The sternal shield (198–216 μm long) is of a characteristic outline, is strongly sclerotized, reticulated and partly punctate (Fig. 50B). The sternal and opisthogastric setae are fine and slender. The anal shield is reticulated and broadly oval, and the three anal setae are simple, the postanal being slightly shorter than the paranals. The peritreme extends to coxa I.

The tectum is trispinate and has dentate lateral margins (Fig. 50C). The chelicera is as in figure 50D. The chaetotaxy of the palp trochanter, genu and tibia is shown in figure 50E: the anterolateral seta on the genu is broad but simple, and the two anterolaterals on the tibia have the distal margin scalloped. The venter of the gnathosoma is as in figure 50F. Legs I, III and IV bear simple setae, those on leg I being the finest. Tarsus IV bears an erect pilose dorsal seta 90–100 μm long. Leg II is shown in detail in figure 50G: the femur bears ventrally a strong erect thumblike spur with a recurved tip, the genu a shorter, more pointed spur, the tibia a rounded spur of intermediate size, and the tarsus bears basally a short conical spur and medially a long tapering spur lying along the segment.

MALE. The idiosoma is strongly sclerotized, reticulated and measures on average 750 μm long × 510 μm wide. The dorsum is divided by a median transverse suture and the two halves may overlap (Fig. 50H). The podonotal region bears about 22 pairs of setae. The majority are very short (up to 23 μm) and fine, but four pairs, *j1* (*c.* 40 μm), *j4, z5* and *r3* (all *c.* 50 μm) are stout and pilose. The opisthonotal region bears similar short fine setae, more numerous posteriorly, and four pairs of stout pilose setae up to *c.* 65 μm in length. A fifth stout pair is situated on the posterior margin.

The tritosternum is apparently lacking and the genital lamina, which is flanked by granular presternal shields, fits closely into the concave anterior margin of the sternogenital shield (Fig. 50I). The sternogenital setae are simple. The opisthogastric region is strongly sclerotized and bears nine pairs of simple setae and one pair of broader pilose setae near to the anus. The three anal setae are short and simple. The peritreme extends to coxa I.

The tectum is trispinate and symmetrical (Fig. 50J). The chelicera is shown in figure 50K: the articulating membrane is provided with a long brushlike process. The chaetotaxy of the palp trochanter, femur and genu is as in figure 50L. The trochanter differs from that of the deutonymph in that the basal seta is considerably stouter. The venter of the gnathosoma is as in figure 50M: the anterior and internal posterior hypostomatic setae are stout. Legs I, III and IV bear short simple setae. Leg II is shown in detail in figure 50N: the femur bears a broad thumblike spur with a short domed auxiliary spur, the genu a tall domed spur, and the tibia a smooth fingertip-like spur.

FEMALE. The podonotal shield (390–410 μm long × 490–550 μm wide) bears 21 pairs of setae of type and arrangement as in the male (*j1, c.* 45 μm, *r3 c.* 90 μm, *j4* and *z5* are intermediate), except that *r4* and *s6* are lacking (Fig. 51A). The opisthonotal shield (430 μm long × 550–590 μm wide) bears only three pairs of stout pilose setae (*c.* 65 μm long) and the small setae are rather less numerous than in the male. Both shields are reticulated.

The tritosternum has a narrow base and pilose laciniae. As in the deutonymph, the granular presternal shields are broad and taper towards each other (Fig. 51B). The sternal shield is reticulated and granular, and setae II are the stoutest and III the finest. The metasternal and genital setae are simple. The genital shield is broad, shallow, and has a long tapered sinuate tip. Two conspicuous but small teeth are visible on the underside of the anterior region of the genital shield and the main components of the endogynium are as shown. The sclerotized opisthogastric region bears seven pairs of setae of which the pair

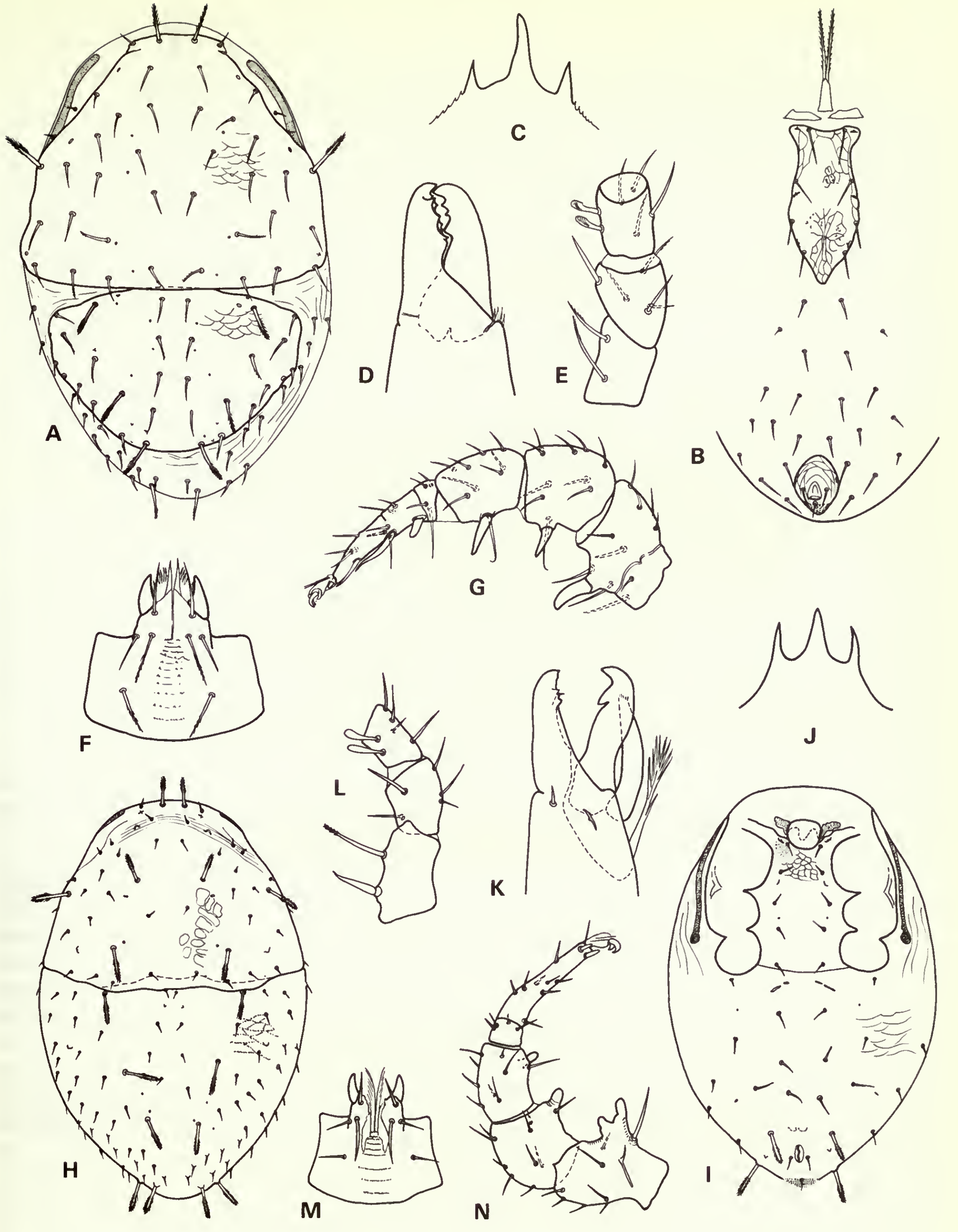

Fig. 50 *Gamasodes spiniger* (Trägårdh), **deutonymph** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma; G leg II: **male** – H dorsum; I venter; J tectum; K chelicera; L palp trochanter, femur and genu; M venter of gnathosoma; N leg II.

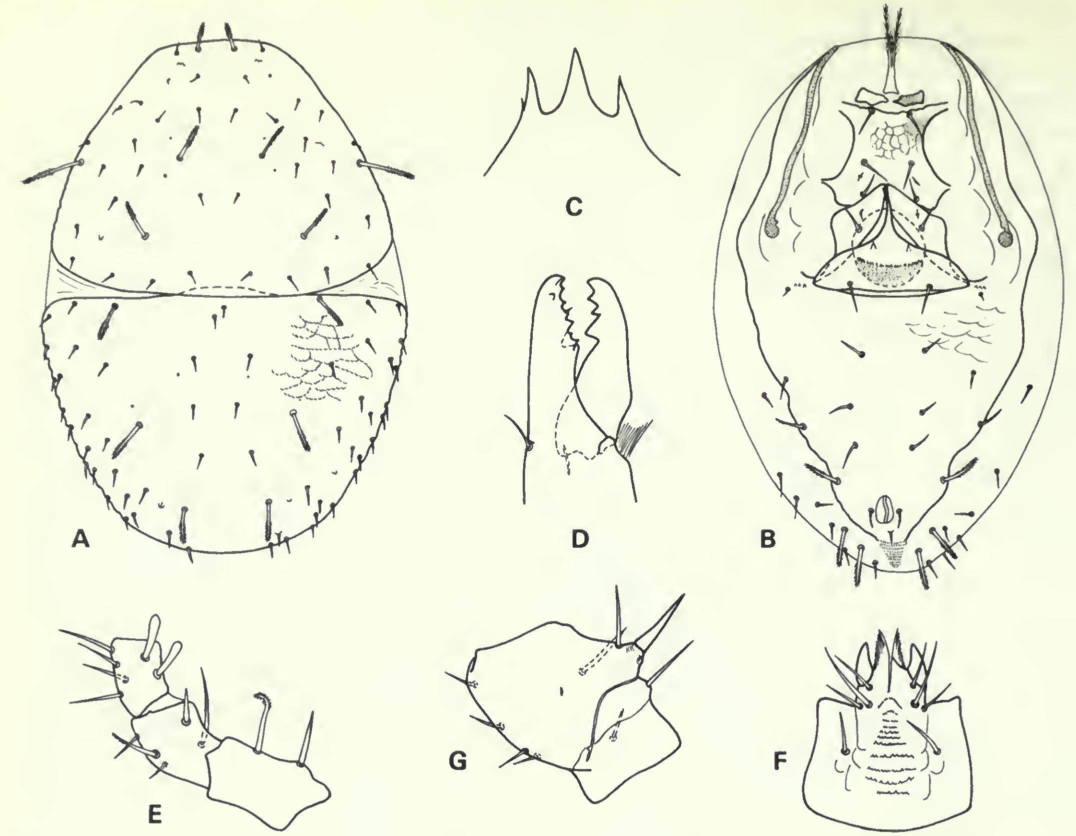

Fig. 51 *Gamasodes spiniger* (Trägårdh), **female** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma; G femur of leg II.

nearest the anus is stout and pilose, as are two further pairs on the adjacent membrane. The three anal setae are fine and short.

The tectum is trispinate similar to the male, slight variation has been observed (Fig. 51C). The chelicera is as in figure 51D. The movable digit has a large conical tooth and two smaller teeth, whilst the fixed digit bears six small teeth. The chaetotaxy of the palp trochanter, femur and genu is shown in figure 51E, and the venter of the gnathosoma in figure 51F: the internal posterior hypostomatic setae are the broadest and the externals the shortest. Leg I bears fine simple setae. On leg II the setae are only scarcely stouter, but the femur bears ventrally a conspicuous stout tapered seta arising from a tubercle (Fig. 51G). Legs III and IV bear almost entirely fine short setae.

Material examined. 28 samples – 35 DNN, 1 ♂, 3 ♀♀.

England: Somerset, Dorset, Isle of Wight, Hampshire, Surrey, London, Berkshire, Buckinghamshire, Essex, Cambridgeshire, Lincolnshire, Lancashire, Westmorland, Yorkshire.

Wales: North. No precise locality. See below.

Scotland: Isle of Mull.

Ireland: Kildare, Meath, Mayo.

In the British Isles this species has been found mainly in association with an animal 'host' such as birds, small mammals, including a fox corpse (Smith, 1975), and insects, but additionally in straw and grassland. A few only have been collected in leaf-litter and mosses. I have examined one deutonymph from seaweed. Previously identified specimens from this habitat have all proved to be *G. fimbriatus* Karg (p. 347).

Distribution. Previous British records of this species are few. Halbert's (1915, 1920) specimens from old nests of puffins *Fratercula arctica* (L.) and black-backed gulls *Larus marinus* L. or *fuscus* L. on The Bills Rocks, Co. Mayo, 21 June 1910, belong to this species, whereas his specimens from under stones on the seashore, Bellacragher Bay, Mulranny, Co. Mayo, 25 September 1913, are *G. fimbriatus.* Hill & Gordon (1945) record deutonymphs of this species (as *Poecilochirus spinipes* Koch) from straw used to stuff the palliasses of American servicemen stationed in North Wales. I have examined some of these specimens. Block (1965) records *spiniger* from *Nardus stricta* L. grassland in Westmorland and I have examined these specimens. Turk (1967) records it from British caves without giving localities, though I have not examined any of his material, whilst Hazelton (1970*b*) records it from a well at Redbourne, Hertfordshire.

Gamasodes spiniger has been recorded from Sweden (Trägårdh, 1910), France (Cooreman, 1954), Belgium (van Daele & Heungens, 1974, 1975), Germany (Oudemans, 1936, Karg, 1961, 1965, 1971), Austria (Leitner, 1946), Switzerland (Schweizer, 1961), Italy (Valle, 1955), U.S.S.R. (Trägårdh, 1904, 1928), Western Siberia (Davydova, 1969, 1976), Poland (Micherdzinski, 1969) and Israel (Shulov, 1957, Costa, 1961, 1963, 1966), from habitats suggesting the various collections are correctly identified.

Gamasodes bispinosus (Halbert)

(Fig. 52A–P)

Gamasoides bispinosus Halbert, 1915: 56.
Gamasodes bispinosus: Strenzke, 1951: 13. Holzmann, 1969: 30. Micherdzinski, 1969: 623. Karg, 1971: 416. Bregetova *et al.*, 1977: 94, 95.

Deutonymph. The podonotal shield (310–320 μm long × 355–360 μm wide) is reticulated, bears 19 pairs of setae, *s2* and *r2* being off the shield (Fig. 52A). All setae are fine and slender except *j1* and *r3* which are stouter, sparsely pilose distally and approximately 28 μm in length. The opisthonotal shield (180–200 μm long × 300–310 μm wide) is also reticulated and bears 12–13 pairs of simple setae. The setae on the posterior membrane are also simple.

The tritosternum has a narrow base and pilose laciniae. It is set close to the elongate presternal shields (Fig. 52B). The sternal shield (198 μm long) is symmetrically shaped and strongly reticulated. The setae are simple. The opisthogastric setae are also simple. The anal shield is reticulated, oval, the three setae are of approximately equal length and simple. The peritreme extends to coxa I.

The tectum comprises three widely spaced prongs, the centre one being forward of the lateral pair. The margin posterior to the lateral prongs is denticulate (Fig. 52C). The chelicera is as in figure 52D. The teeth are not so well separated as in either *spiniger* or *fimbriatus.* The chaetotaxy of the palp femur and genu is as in figure 52E, and the venter of the gnathosoma in figure 52F. Leg I bears fine simple setae. Leg II is shown in detail in figure 52G. The femur bears a forward-projecting thumblike ventral spur and at its inner angle is a second similar but smaller spur. The genu bears a single tapered peglike spur, whilst the tibia is devoid of spurs, but bears ventrally a stout seta. The tarsus bears proximally a peglike spur and medially a long tapering spur lying against the segment. Leg III bears simple setae which are stoutest on the tarsus, whilst leg IV bears similar setae with the addition of an erect pilose dorsal seta *c.* 65 μm long on the tarsus.

Male and female. Adults have not been collected in the British Isles. Strenzke (1951) figured the deutonymph, male and female from specimens collected on the Baltic coast. Holzmann (1969) also figured both the adult sexes. Figures 52H–K of the male and 52L–P of the female are based on Strenzke's paper. The idiosoma of the male measures 750–850 μm long × 500–550 μm wide, and of the female 950 μm long × 750 μm wide.

Material examined. 4 samples – 5 DNN.

england: One deutonymph on *Limosina* sp. (Diptera) in a garden, Madeley, Staffordshire, 25 April 1937, coll. H. Britten; one deutonymph in tidal debris at high water mark, Yantlet Creek, Allhallows, N. Kent, 29 July 1956, coll. K. H. Hyatt.

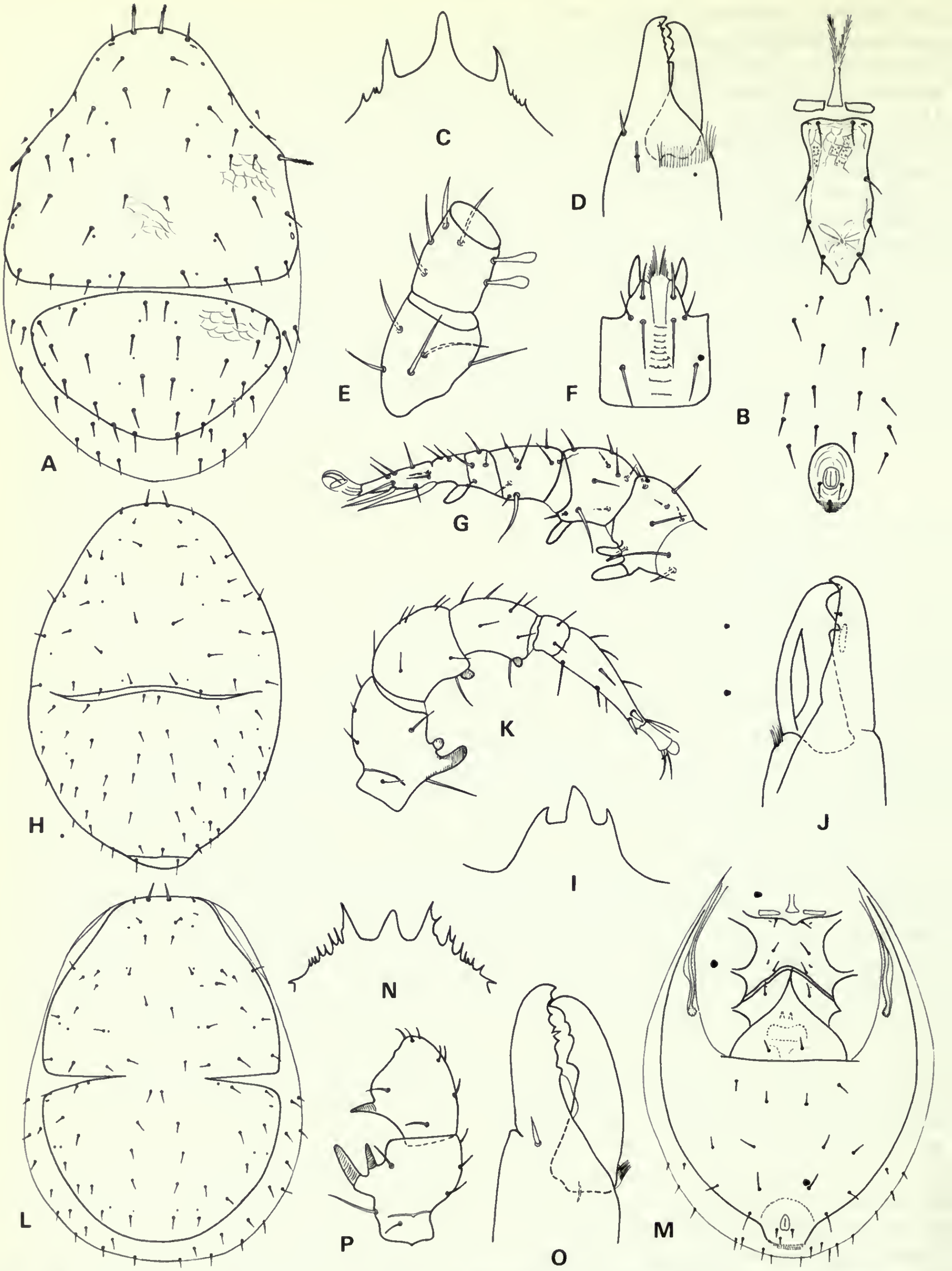

Fig. 52 *Gamasodes bispinosus* (Halbert), **deutonymph** – A dorsum; B venter; C tectum; D chelicera; E palp femur and genu; F venter of gnathosoma; G leg II: **male** – H dorsum; I tectum; J chelicera; K leg II: **female** – L dorsum; M venter; N tectum; O chelicera; P femur and genu of leg II. H–P after Strenzke, 1951.

WALES: Two deutonymphs in seaweed, Menai Straits, Bangor, Caernarvonshire, 23 August 1976, coll. Mrs M. J. Morgan.

IRELAND: One deutonymph from grassland, Celbridge, Co. Kildare, coll. G. O. Evans.

DISTRIBUTION. Halbert (1915) described this species from deutonymphs collected in moss near Lough Fenagh, Co. Mayo, and in moss from Poyntzpass, Co. Armagh, but since then there have been no British records.

It has been recorded from Germany (Strenzke, 1951, Holzmann, 1969, Karg, 1961, 1965, 1971), Austria (Franz, 1943, Strenzke, 1951), U.S.S.R. (Pinchuk, 1976) and Western Siberia (Davydova, 1969, 1976). Habitats range from the sea coast and in brackish habitats to rotting vegetation and humus in damp meadows and woods.

Davydova (1973) has described from Western Siberia a second species of *Gamasodes,* namely *G. micherdzinskii,* in which the deutonymph bears, like *bispinosus,* a double spur on femur II and the adults similar spurs. The main difference between the two species appears to be that *micherdzinskii* has considerably longer dorsal idiosomal setae than *bispinosus.*

Gamasodes fimbriatus Karg
(Figs 53A–K; 54A–F)

Gamasodes fimbriatus Karg, 1971: 414. Bregetova *et al.,* 1977: 94.
Gamasoides spinipes (C. L. Koch), Halbert, 1915: 55; 1920: 119, in part.

DEUTONYMPH. The podonotal shield averages 324 μm long × 372 μm wide and bears 19–21 pairs of setae (Fig. 53A). Setae *j1, j4, z5* and *r3* are stout and pilose, the remainder very short (max. 20 μm) and simple but thornlike. Setae *s2* and *r2* may be on or off the shield. The opisthonotal shield averages 216 μm long × 300 μm wide and bears 14 pairs of setae of which three, *Z1, Z3* and *J5,* are pilose, stouter (*Z1* being the more so) and the remainder short and thornlike. Both shields are well sclerotized and entirely reticulated. The posterior membrane bears only short thornlike setae.

The tritosternum has a narrow base and pilose laciniae. It is set close to the presternal shields which almost meet medially (Fig. 53B). The sternal shield (228 μm long) is symmetrically shaped, and the setae are slender and simple. The opisthogastric setae are short and two pairs in the anal region are pilose distally. The anal shield is oval and reticulated with the anus situated midway. The anal setae are fine and short. The peritreme extends to coxa I.

The tectum comprises a broad central pointed prong which is flanked by a backwards-sloping toothed ridge of apparently regular pattern (Fig. 53C). The chelicerae, which have one large and two smaller teeth on the movable digit and four or five well-seperated teeth on the fixed, are similar to those of the female (Fig. 54D). The chaetotaxy of the palp trochanter, femur and genu, and also the venter of the gnathosoma, are as in the female (Figs 54E and F). The setae of leg I are mainly short and fine with few only pilose. Leg II is shown in detail in figure 53D. The ventral spur on the femur is slender, scarcely tapering and almost straight; that on the genu and tibia are similar but shorter, whilst the proximal spur on the tarsus is slightly tapering. Medially the tarsus bears a long tapering spur lying along the segment and distally two broad tapered ventral setae. Leg III bears stouter setae than leg I, especially on the tibia and tarsus, whilst on leg IV the setae are similar to those on leg III, but the tarsus bears an erect pilose dorsal seta 85–90 μm long.

MALE. The idiosoma is usually less heavily sclerotized than in *G. spiniger.* It measures 804–850 μm long × 468–500 μm wide and is divided dorsally by an undulating transverse suture (Fig. 53E). The podonotal region bears 23 pairs of setae, the majority of which are very short (25 μm max.), but four pairs, *j1* (*c.* 45 μm), *j4* (*c.* 55 μm), *z5* (*c.* 63 μm) and *r3* (*c.* 75 μm), are stout and pilose. The opisthonotal region bears similar short setae with two pairs, *Z1* and *Z3,* stout, pilose and measuring approximately 55 μm in length.

The tritosternum is extremely small and is just visible beneath an anterior membrane protruding from the genital lamina (Fig. 53F). The presternal shields are indistinct. The

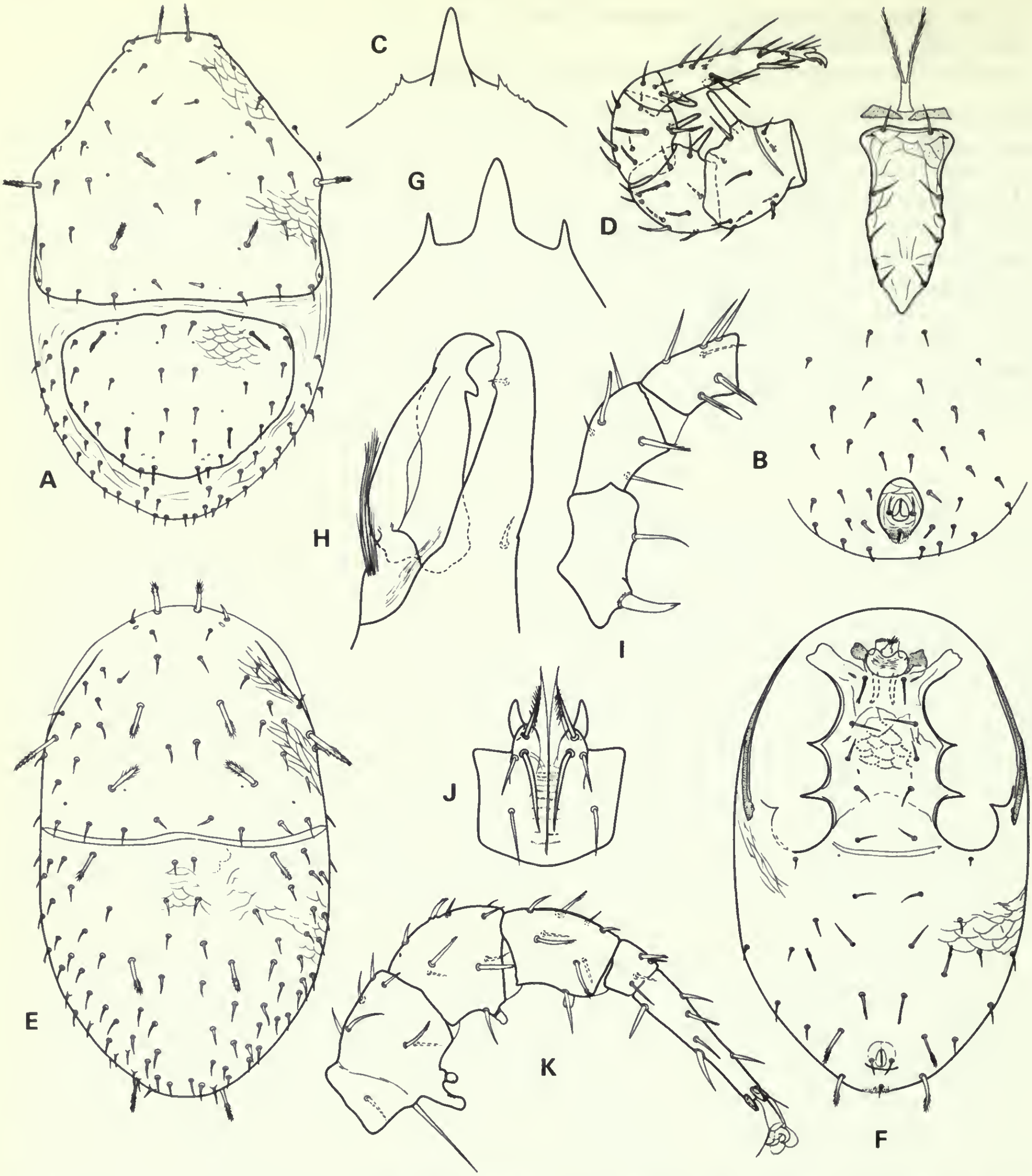

Fig. 53 *Gamasodes fimbriatus* Karg, **deutonymph** – A dorsum; B venter; C tectum; D leg II: **male** – E dorsum; F venter; G tectum; H chelicera; I palp trochanter, femur and genu; J venter of gnathosoma; K leg II.

sternal setae are fine, slender and in the specimen figured one seta I is bifid distally. Several of the opisthogastric setae are pilose distally and two posterior pairs are similar to the stout dorsal setae and measure *c.* 63 μm. The anal setae are simple. The peritreme extends to coxa I.

The tectum has a broadly pointed centre prong and is flanked posteriorly by a pair of small short, pointed prongs (Fig. 53G). The chelicera is shown in figure 53H: as in *spiniger* the articulating membrane is provided with a long brushlike process. The chaetotaxy of the palp trochanter, femur and genu is shown in figure 53I. the basal seta of the trochanter is much stouter than in either the deutonymph or the female. The venter of the gnathosoma is shown in figure 53J. The anterior and internal posterior hypostomatic setae are stout with the latter being the longest. The setae of leg I are mainly simple although a number of the dorsal setae and some ventral are pilose in their distal thirds. Leg II is shown in detail in figure 53K. The femur bears ventrally a small thumblike spur with a domed tuberculated auxiliary spur, the genu bears a domed spur also arising from an eminence, and the tibia bears a fingertip-like spur only. The setae are relatively short, stout, and some are pectinate to one side of their tips. Legs III and IV bear short setae of which a number are pilose distally, often on one margin of the curved tip.

FEMALE. The podonotal shield (380–420 μm long × 468–540 μm wide) bears 21 pairs of setae whose arrangement and relative lengths are as in the male, except that *r4* are situated off the shield. Setae *j1* are *c.* 45 μm, *j4 c.* 50 μm, *z5 c.* 65 μm and *r3 c.* 75 μm, and the right *z6* is duplicated (Fig. 54A). The opisthonotal shield (330–420 μm long × 420–580 μm wide) bears three pairs of stout pilose setae approximately 57 μm in length, although in one of the specimens examined (Fig. 54A) an extra unpaired stout seta is present, and the remainder are simple, rather peglike, and vary in number (cf. Figs 54A and B).

The tritosternum has a narrow base and pilose laciniae. It is flanked by wedge-shaped granular presternal shields (Fig. 54C). The sternal shield is granular, setae I and II are the stoutest. The genital shield is broad, shallow, and has a long tapered tip. Two small teeth are visible on the underside of the anterior margin of the genital shield and the main components of the endogynium are shown. The sclerotized opisthogastric region bears seven pairs of setae of which the pair nearest the anus is stout and pilose, as are two further pairs on the adjacent membrane. The three anal setae are fine and short. The peritreme extends to coxa I.

The tectum is generally as in the male (Fig. 53G), only minor irregularities in outline having been observed. The chelicera is shown in figure 54D, the chaetotaxy of the palp trochanter, femur and genu in figure 54E, and the venter of the gnathosoma in figure 54F; the internal posterior rostral setae are the longest and stoutest. The setae of leg I are fine and simple. On leg II the setae are generally a little stouter, but the femur bears ventrally a stout tapered seta similar to that of *spiniger.* Legs III and IV bear stouter setae than *spiniger* and many have the distal portion finely pilose.

MATERIAL EXAMINED. 20 samples – 13 DNN, 21 ♂♂, 23 ♀♀.
ENGLAND: Isles of Scilly, Cornwall, Kent, Essex, Northumberland.
WALES: Caernarvonshire, Anglesey.
SCOTLAND: Argyllshire, Outer Hebrides (Harris, Lewis).
IRELAND: Clare, Mayo.

DISTRIBUTION. *Gamasodes fimbriatus* has not previously been recognized in the British literature and is recorded for the first time. Halbert's (1915, 1920) records of *Gamasoides spinipes* comprise two species, *Gamasodes spiniger* and *G. fimbriatus.* His specimens from old nests of seabirds are referrable to *spiniger* (*q. v.*), but those from under stones on the seashore, Bellacragher Bay, Mulranny, Co. Mayo, 25 September 1913, are *fimbriatus.* The nineteen other samples examined here are from debris or under stones on the seashore.

Elsewhere this species is known only from the Baltic coast (Karg, 1971).

Genus ***POECILOCHIRUS*** G. & R. Canestrini

Poecilochirus G. & R. Canestrini, 1882. *I Gamasi Italiani. Monografia.* Padova: 21.
Gamasoides Berlese, 1904. *Redia* **1**: 280.

TYPE SPECIES. *Poecilochirus carabi* G. & R. Canestrini, 1882.

Dorsal shield of male entire, with transverse suture; female and deutonymph with separate podonotal and opisthonotal shields, although partial fusion may occur in some females. Setae *z5* of dorsal hexagon similar to setae *j5* and *j6* in females, considerably longer and/or stouter in deutonymphs and males. Tritosternum normal, biramous, that of male closely associated with genital orifice and with base shortened. Junction between sternal and

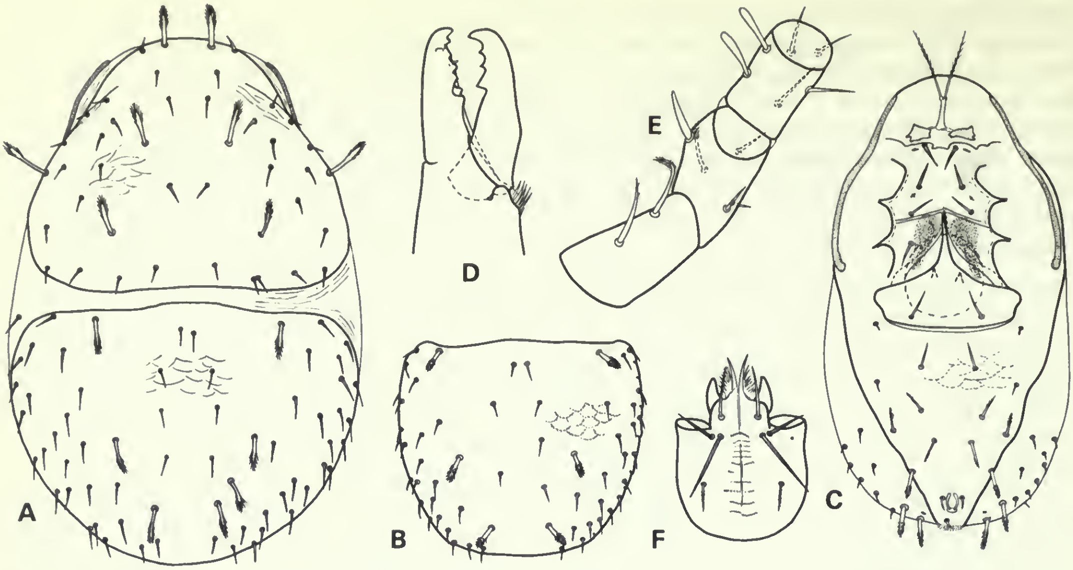

Fig. 54 *Gamasodes fimbriatus* Karg, **female** – A dorsum; B variation in opisthonotal shield; C venter; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma.

metasternal shields of female oblique. Genital shield of female triangular. Sternal shield of deutonymph usually showing transverse granular band between setae I and II. Opisthogastric shield in female with usually less than 15 pairs of setae; opisthogastric region in the male and deutonymph with considerably more. Setae *al* of palp femur and al_1 and al_2 of palp genu spatulate. Chelicerae of deutonymph sometimes with membraneous process at tip of fixed digit. Corniculi of male usually hooked, of female and deutonymph small and tapered. Legs of deutonymph and female normally without spurs; only leg II of male spurred. Lobes of pulvilli normal, rounded.

Poecilochirus carabi G. & R. Canestrini
(Figs 55A–M; 56A–M)

Poecilochirus Carabi G. & R. Canestrini, 1882: 56. Vitzthum, 1930*b*: 392. Micherdzinski, 1969: 629. Holzmann, 1969: 7. Karg, 1971: 420. Bregetova et al., 1977: 99, 101, 102.

Gamasoides carabi: Halbert, 1915: 55.

Poecilochirus necrophori Vitzthum, 1930*b*: 392. Cooreman, 1943: 15. Neumann, 1943: 1–21. Turk & Turk, 1952: 480. Micherdzinski, 1969: 633. Holzmann, 1969: 7. Karg, 1971: 419. Bregetova *et al.*, 1977: 99, 101. **Syn. nov.**

Poecilochirus fucorum (De Geer) sensu Berlese, 1892*b*, Fasc. 69, No.4, figs 1–4.

Gamasoides eurasiaticus Trägårdh, 1937: 8. Willmann, 1939*a*: 438. Micherdzinski, 1969: 633. Davydova, 1976: 103.

Gamasus stygius Hull, 1918: 85. Holzmann, 1969: 7. Micherdzinski, 1969: 629.

The deutonymphs of *Poecilochirus carabi* G. & R. Canestrini and *P. necrophori* Vitzthum fall into groups that are separated by most authors who have considered this genus (e.g. Vitzthum, 1930*b*, Micherdzinski, 1969 and Holzmann, 1969) on the single criterion of whether or not the transverse band in the anterior half of the sternal shield is produced up and down the margins of the shield. Karg (1971) separates the two species on their dorsal chaetotaxy and considers the emphasis on the sternal band to be a useless character. He also suggests that they may be subspecies. Vitzthum, around the time that he described *P. necrophori* (1930*b*), identified a single deutonymph in the British Museum collection from Bagley, Berkshire, as *P. carabi.* In this specimen the dark sternal band is at first glance without lateral extensions, but on closer examination, and by varying the intensity of the illumination, these extensions are visible although paler than the central portion. The many British specimens examined, plus two large samples from France, show a wide degree of variation in both the extent and intensity of the sternal band, and in the dorsal chaetotaxy as enumerated by Karg. Therefore, in view of the wide range of variation encountered and the apparently arbitrary distinctions on which workers subsequent to Vitzthum have based their identifications, I feel disposed to consider *necrophori* to be a junior synonym of *carabi*.

Additionally, with both *Poecilochirus eurasiaticus* Trägårdh, 1937 and *P. trebinjensis* Willmann, 1940 (which are not recorded from the British Isles) it seems that their status is based on equally variable characters as has been suggested already by Micherdzinski (1969) and they also may well be synonymous with *carabi*.

Trägårdh (1937) based his description of *eurasiaticus* on specimens from both Swedish Lappland and southern Mongolia, but his figures, especially of the dorsum, are lacking in detail and do not match his description, therefore without examining specimens it is not possible to pass judgment. However, Willmann (1939*a*) considers *eurasiaticus* to be synonymous with *necrophori*, whereas Micherdzinski (1969) considers only the Lappland specimens to be synonymous with *necrophori*. Davydova (1976) simply lists *eurasiaticus* as a synonym of *necrophori* without comment. Willmann (1940) based his description of *trebinjensis* on seven deutonymphs and a single male from Jugoslavia, and he noted that the nymphs closely resembled *necrophori* but were larger. Micherdzinski (1969) only commented that in spite of the wide geographical range of the deutonymphs of *Poecilochirus*-species, their differences were minute, and that the single specimen he had from Kashmir agreed with Willmann's description of *trebinjensis*. As both *eurasiaticus* and *trebinjensis* post-date *necrophori* their true status is of no direct consequence at present in relation to the British fauna, except to emphasize the need for detailed studies of their life histories to be carried out and for the range of variation within populations to be documented.

PROTONYMPH. Only one protonymph has been examined, but it compares favourably with the figures of Neumann (1943), Holzmann (1969) and Micherdzinski (1969), who also figured the larva. Only Holzmann, however, outlined the dorsal shields. Figures 55A–G show respectively the dorsum, the anal region, the tectum, the venter of the gnathosoma, the chelicera, the right palp trochanter, femur and genu, and the left tibia and tarsus IV.

DEUTONYMPH. The podonotal shield (576–670 μm long × 720–930 μm wide) is well sclerotized, granular and entirely reticulated (Fig. 55H). It bears 21 pairs of setae of which *z1*, *s1* and *s2* are very short (*c.* 14 μm) and peglike. The remaining setae are stout and of varying lengths with *z5* (*c.* 270 μm) and *r3* (*c.* 380 μm) the longest. The opisthonotal shield (420–480 μm long × 720–860 μm wide) is of similar texture to the podonotal shield. It bears 13 pairs of homogeneous setae of variable length which have traces of pilosity at their tips. The posterior membrane bears short setae.

The tritosternum has a narrow base and pilose laciniae. It is flanked by dark elongate presternal shields. The sternal shield (335–430 μm long) is granular, reticulated, and has a transverse darkly sclerotized band between setae I and II, which may extend anteriorly or posteriorly by varying amounts and intensities (Fig. 55I). The endopodal shields are generally darkly sclerotized, especially at coxae IV. The opisthogastric setae are fine and simple. The anal shield is elliptical, reticulated and granular, and the paranal setae are slender, the postanal stouter. The peritreme extends to coxa I.

The tectum comprises a sharply tapered central prong flanked by a pair of inwardly curved side prongs (Fig. 55J). The chelicera is shown in figure 55K; the membraneous process at the tip of the fixed digit is fairly constantly shaped but may be broken off. The chaetotaxy of the palp trochanter, femur and genu is as in figure 55L, with the anterolateral setae on the femur and genu alike, broadly spatulate distally, whilst the distal dorsal seta on the femur is noticeably stout and finely pilose in its distal half. The venter of the gnathosoma is shown in figure 55M. The corniculi are partly hidden by the hypostome. All leg setae are

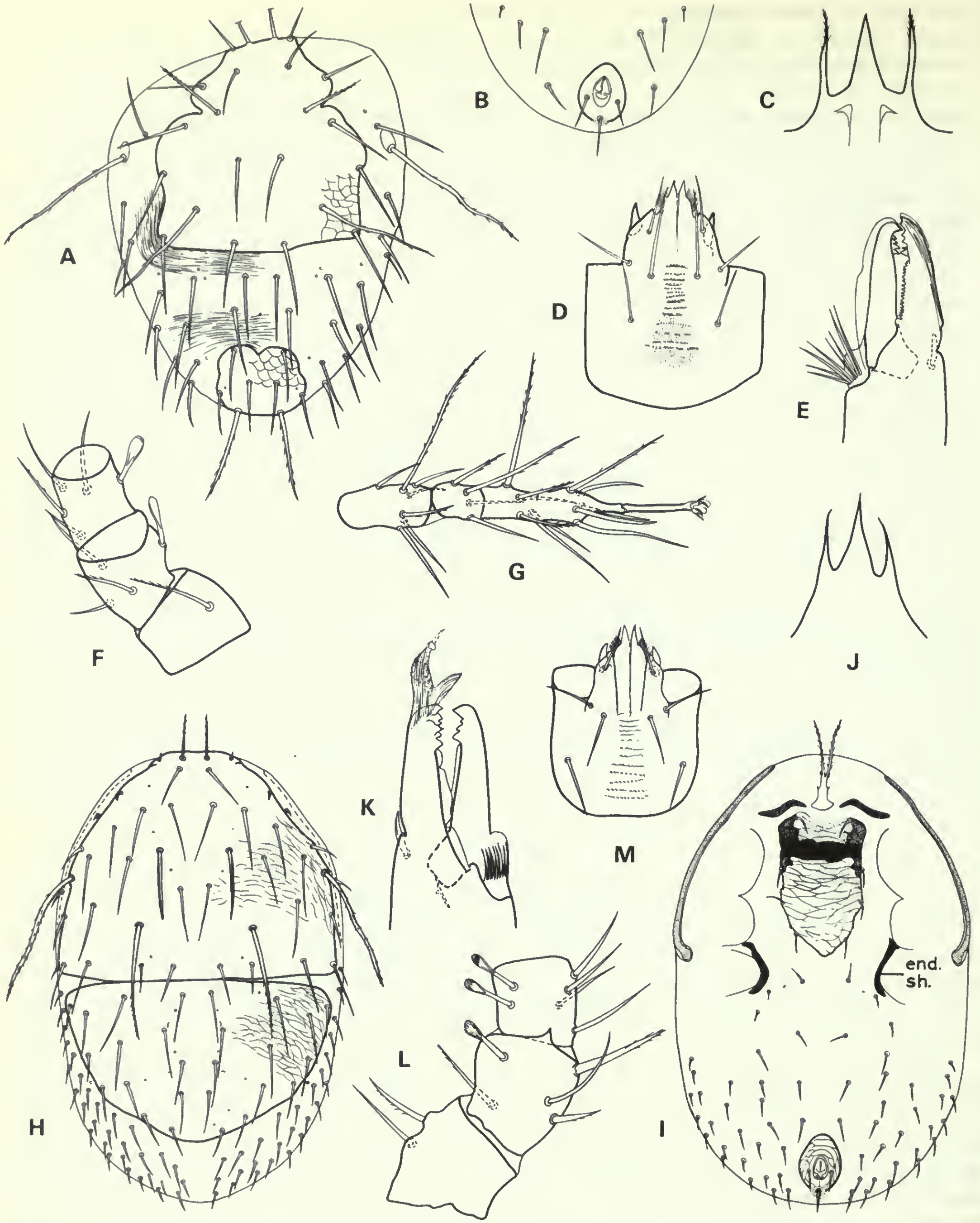

Fig. 55 *Poecilochirus carabi* G. & R. Canestrini, **protonymph** – A dorsum; B anal region; C tectum; D venter of gnathosoma; E chelicera; F palp trochanter, femur and genu; G tibia and tarsus of leg IV: **deutonymph** – H dorsum; I venter; J tectum; K chelicera; L palp trochanter, femur and genu; M venter of gnathosoma. *end. sh.*, endopodal shield.

strong and many are very finely pilose or rasp-like. Legs II–IV each bear an erect dorsal seta distally on the femur, that on femora III and IV being the longest (250 μm and 350 μm respectively).

MALE. The idiosoma is well sclerotized and entirely reticulated. It measures 1200–1300 μm long × 780–840 μm wide and is divided dorsally by a median transverse suture (Fig. 56A). The podonotal region bears 22 pairs of mainly stout and finely pilose setae of which three pairs, *j4, z5* and *r3*, are the longest. Setae *z1, s1* and *s2* are very short, *s1* being only *c.* 15–18 μm. The opisthonotal region bears shorter stout pilose setae of more even length.

The tritosternum has a short narrow base and pilose laciniae (Fig. 56B). The venter is entirely covered by a reticulated holoventral shield. The sternal setae are the stoutest and longest, all are essentially simple, except the postanal which is long and finely pilose. The peritreme extends to coxa I.

The tectum comprises a broad denticulate process terminating in a long slender pointed tip (Fig. 56C). The chelicera is shown in figure 56D: the fixed digit lacks the membraneous process at the tip. The chaetotaxy of the palp trochanter, femur and genu is as in figure 56E. The three anterolateral setae on the femur and genu are alike, the setae on the trochanter arise from strong tubercles. The venter of the gnathosoma is as in figure 56F. The corniculi are indented on their inner margins and the tips are hooked; the anterior hypostomatic setae are the stoutest and the external posteriors and the palpcoxals are finely pilose. Many of the leg setae are stout and/or finely pilose. Coxa I bears a short conical spurlike seta dorsally and the femur a similar but longer one. Leg II is shown in detail in figure 56G. Legs III and IV bear mainly stout but pointed setae with none conspicuously long.

FEMALE. The podonotal shield (700–750 μm long × 880–1100 μm wide) is well sclerotized and reticulated. It bears 21 pairs of setae all of which are stout, with the majority having at least the tips finely pilose or squarrose (Fig. 56H). Setae *j1* and *r3* are the longest and *z1, s1* and *s2* very short. The opisthonotal shield is of similar structure and measures 900–1020 μm long × 1080–1390 μm wide. The setae, which number about 40 pairs, are all of similar form to those on the podonotal shield, but slightly longer.

The tritosternum has a narrow base and pilose laciniae and is flanked by elongate curved presternal shields (Fig. 56I). The sternal and metasternal shields are generally rather indistinctly demarcated although well reticulated. Sternal setae II are the stoutest. The genital shield is pointed anteriorly but merges posteriorly with the opisthogastric shield. The opisthogastric setae are slender and simple. The anus is situated well in advance of the posterior margin of the often irregular opisthogastric shield which may be indented laterally. The paranal setae are short, fine, and the postanal stouter and long. The peritreme extends to coxa I.

The tectum is shown in figure 56J. It comprises a long tapered eminence with angular serrated margins. The chelicera is as in figure 56K, with additionally the tip of the second fixed digit of the same specimen. The fixed digit lacks the membraneous process at the tip. The chaetotaxy of the palp trochanter, femur and genu is as in figure 56L. The three anterolateral setae on the femur and genu are alike. The venter of the gnathosoma is shown in figure 56M. Except for fine setae only on tarsus I, the majority of the leg setae are stout and finely pilose distally. No long setae are present.

MATERIAL EXAMINED. 162 samples – 1 PN, *c.* 3130 DNN, 5 ♂♂, 19 ♀♀.

ENGLAND: Cornwall, Somerset, Gloucestershire, Hampshire, Surrey, Sussex, Buckinghamshire, Berkshire, Hertfordshire, Bedfordshire, Suffolk, Norfolk, Lincolnshire, Shropshire, Derbyshire, Cheshire, Lancashire, Westmorland, Yorkshire, Northumberland (Farne Islands), Durham.

WALES: Glamorganshire, Pembrokeshire, Skomer, Cardiganshire, Montgomeryshire, Caernarvonshire.

SCOTLAND: West Lothian, Dunbartonshire, Perthshire, Arran, Outer Hebrides (Barra), Fair Isle.

IRELAND: Kerry (Great Blasket), two deutonymphs with no locality.

This species has been found in the British Isles, mainly in the deutonymph stage, almost

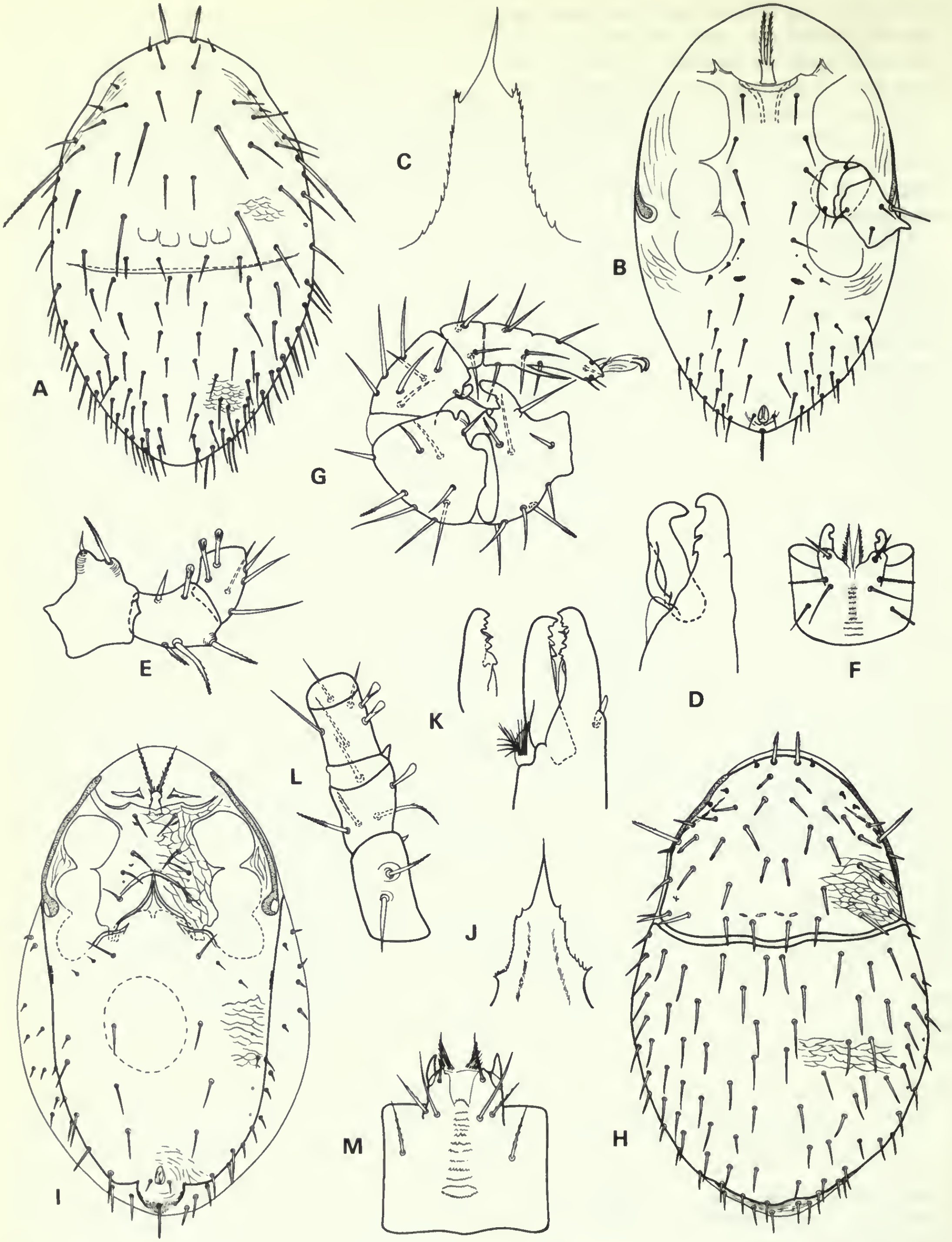

Fig. 56 *Poecilochirus carabi* G. & R. Canestrini, **male** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma; G leg II: **female** – H dorsum; I venter; J tectum; K chelicera, with additionally the second fixed digit of the same specimen; L palp trochanter, femur and genu; M venter of gnathosoma.

exclusively on carrion beetles of the genus *Nicrophorus* (Silphidae). A small number of samples are from beetles of other genera, viz. *Aphodius* (Scarabaeidae), *Carabus* and *Pterostichus* (Carabidae), whilst a few are from dead birds and small mammals. One specimen of *Nicrophorus humator* (Gleditsch) from North Hill, Launceston, Cornwall, 26 July 1974, was carrying 1486 deutonymphs of this species, together with 107 deutonymphs of *P. subterraneus,* 11 females of *Macrocheles glaber* (Müller) (Macrochelidae) and three females of *Alliphis halleri* (G. & R. Canestrini) (Eviphididae). The few adults examined are from red squirrel *Sciurus vulgaris* L., a dead mole *Talpa europaea* L., field-voles *Microtus agrestis* (L.) and a common shrew *Sorex araneus* L.

DISTRIBUTION. Previous British records are from the Tyne Province (Hull, 1918), Clare Island, Co. Mayo (Halbert, 1915), Isle of Lewis, Outer Hebrides (Hora, 1934), Cheshire, Lancashire, Cornwall and Ireland (no precise locality, but the same material as that quoted above for Ireland (Turk & Turk, 1952), and the Farne Islands (Springett, 1968). I cannot confirm the record from the Spurn Peninsula, Yorkshire (Braham & Murgatroyd, 1953).

Poecilochirus carabi is recorded from Belgium (Willmann, 1935, Leruth, 1939, Cooreman, 1943, van Daele & Heungens, 1974), Germany (Kneissl, 1914, Neumann, 1943, Holzmann, 1969, Karg, 1971), Switzerland (Schweizer, 1961), Italy (Schweizer, 1961), Poland (Willmann, 1939*a*, Starzyk, 1967), Romania (Cooreman, 1951), Czechoslovakia (Willmann, 1954, 1956, Mrciak & Rosický, 1956), Lapland (Trägårdh, 1937), U.S.S.R. (Bregetova, 1956, Vysockaja & Bregetova, 1957, Belozerov, 1957, Rudyshyn & Bilokon, 1961, Pirjanik, 1962, Pinchuk, 1976), Western Siberia (Davydova, 1969, 1976) and China (Vitzthum, 1930*b*).

Poecilochirus austroasiaticus Vitzthum
(Figs 57A–F; 58A–G; 59A–F)

Poecilochirus austroasiaticus Vitzthum, 1930*b*: 392. Willmann, 1939*a*: 438. Holzmann, 1969: 7. Micherdzinski, 1969: 665. Karg, 1971: 419. Bregetova *et al.*, 1977: 99, 101, 102.
Poecilochirus nordi Davydova, 1969: 29; 1976: 109. Bregetova *et al.*, 1977: 101, 102. **Syn. nov.**

DEUTONYMPH. The podonotal shield (432–460 μm long × 480–492 μm wide) is well sclerotized and entirely reticulated (Fig. 57A). It bears 21 pairs of setae, all are stout and relatively long with the following exceptions: *z1* very short and *s1, s2* and *r2* short but increasing in length progressively; *r3* the longest (*c.* 185 μm) and clearly but sparsely pilose, *z5* almost as long. Several other setae may also be pilose at their tips. The opisthonotal shield (276–330 μm long × 400–456 μm wide) is of similar texture to the podonotal shield. It bears 13 pairs of homogeneous setae with traces of pilosity at their tips. The posterior membrane bears shorter simple setae.

The tritosternum has a narrow base and pilose laciniae. It is flanked by dark elongate presternal shields (Fig. 57B). The sternal shield (264–280 μm long) is granular, reticulated, and has a transverse darkly sclerotized band between setae I and II, which may extend anteriorly and posteriorly by varying amounts and intensities. The sternal setae are fine and slender. The endopodal shields at coxae IV are conspicuous and strongly sclerotized. The opisthogastric setae are fine and simple. The anal shield is elliptical, reticulated anteriorly, and the anal setae are simple, the postanal being the longest. The peritreme extends to coxa I.

The tectum comprises three slender pointed prongs, the lateral pair curving inwards (Fig. 57C). The chelicera is shown in figure 57D: only a rudimentary membranous process is present at the tip of the fixed digit. The chaetotaxy of the palp trochanter, femur and genu is as in figure 57E: the anterolateral setae on the femur and genu are alike. The venter of the gnathosoma is as in figure 57F. The corniculi are partly concealed by the anterior reaches of the hypostome. The leg setae are generally slender, often with fine pilosity at their tips. Single long stout dorsal setae are present on femora III (*c.* 120 μm) and IV (*c.* 145 μm).

MALE. The idiosoma is entirely reticulated and measures 792–828 μm long × 492–540 μm wide. It is divided dorsally by a median transverse suture (Fig. 58A). The podonotal region

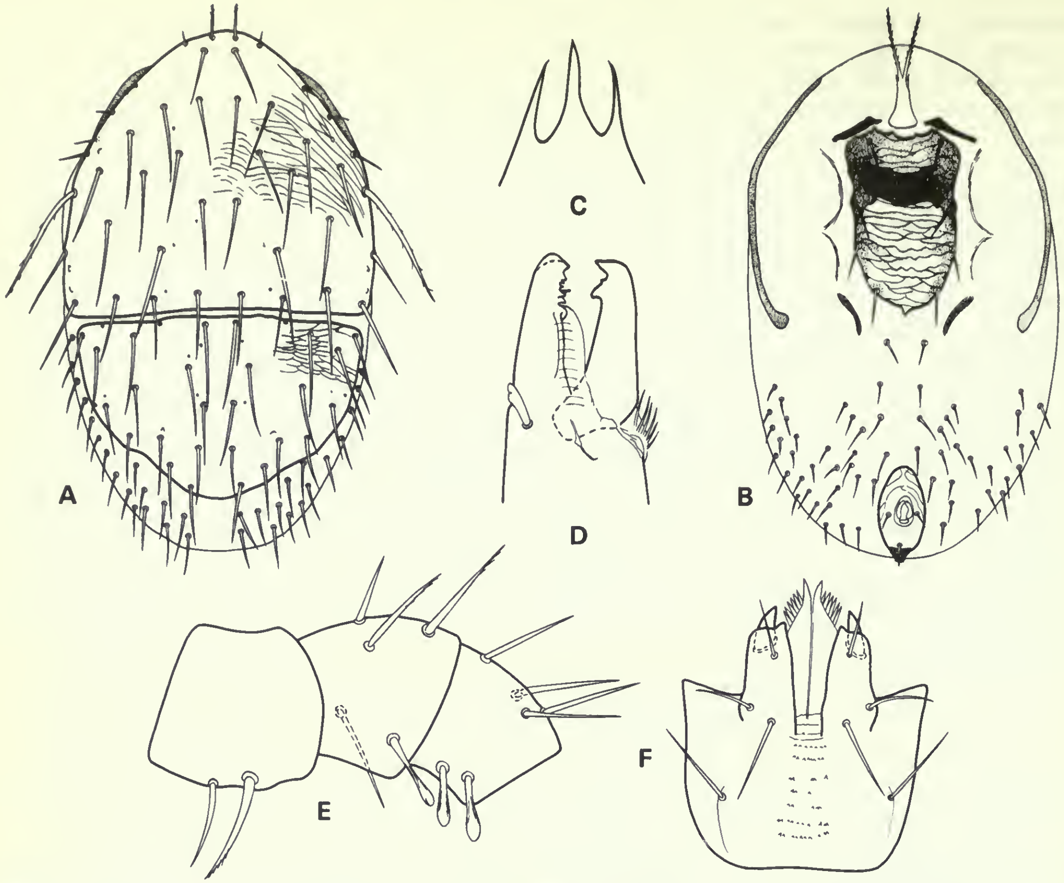

Fig. 57 *Poecilochirus austroasiaticus* Vitzthum, **deutonymph** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma.

bears 22 pairs of setae whose arrangement and type are as in the deutonymph, with the addition of *r4* which are situated on the shield. The opisthonotal region also bears similar setae to the deutonymph, except that the posterior setae are longer than those on the membrane in that instar.

The tritosternum has a short narrow base and pilose laciniae (Fig. 58B). The venter is entirely reticulated and most setae are relatively long and slender. The postanal seta is more than twice the length of the paranals and is much stouter. The peritreme extends to coxa I.

The tectum comprises a tapering flat process with a single pointed tip which may be flanked by a pair of smaller points (Fig. 58C). The chelicera is shown in figure 58D: the fixed digit is without a membraneous process at the tip. The chaetotaxy of the palp trochanter, femur and genu is shown in figure 58E. The three anterolateral setae on the femur and genu are alike. The venter of the gnathosoma is shown in figure 58F. The corniculi are swollen and strongly hooked distally, whilst the palpcoxal setae are stout and pilose. There are no markedly stout or long setae on legs I, III and IV. Leg II is shown in detail in figure 58G.

FEMALE. The podonotal shield (480–528 μm long × 600–648 μm wide) is well sclerotized, granular, entirely reticulated and partly fused with the opisthonotal shield (Fig. 59A). It bears 21 pairs of setae which are generally shorter than in the male and deutonymph. Most are finely pilose at their tips, and *s1,* and sometimes *s2,* may be off the shield. Some specimens have an additional unpaired seta between *s5* and *s6,* this is shown dotted in the figure. The opisthonotal shield is of the same structure as the podonotal and measures

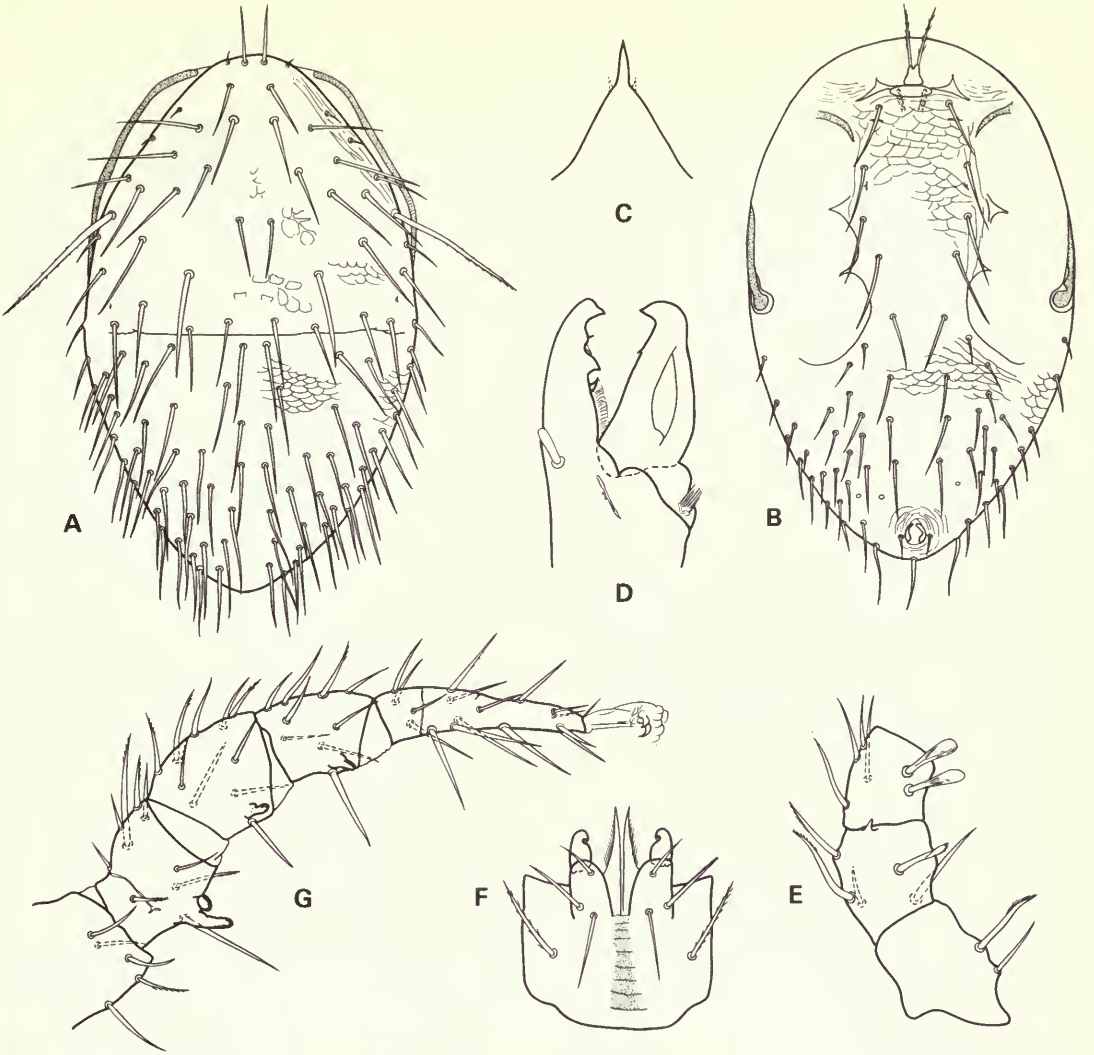

Fig. 58 *Poecilochirus austroasiaticus* Vitzthum, **male** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma; G leg II.

516–552 μm long × 720–804 μm wide. It bears approximately 40 pairs of setae similar to those on the podonotal shield. As in figure 59A, the two shields may be partly fused.

The tritosternum has a narrow base and pilose laciniae. It is flanked by wedge-shaped presternal shields (Fig. 59B). The sternal shield is granular and well reticulated with the centre portion darker. The genital shield is pointed anteriorly, whilst posteriorly it merges with the opisthogastric shield. The latter is irregular in outline and the opisthogastric setae are not all symmetrically placed. The surrounding membrane bears generally shorter setae than those on the shield. The paranal setae are short, the postanal is long. The peritreme extends to coxa I.

The tectum is shown in figure 59C. It comprises a slender central tip flanked by two small prongs. The chelicera is as in figure 59D, the palp trochanter, femur and genu in figure 59E. The venter of the gnathosoma is shown in detail in figure 59F. The internal posterior hypostomatic and palpcoxal setae are the longest and finely pilose, the corniculi are partly concealed by the anterior of the hypostome. The leg setae are generally finer than in *P. carabi*.

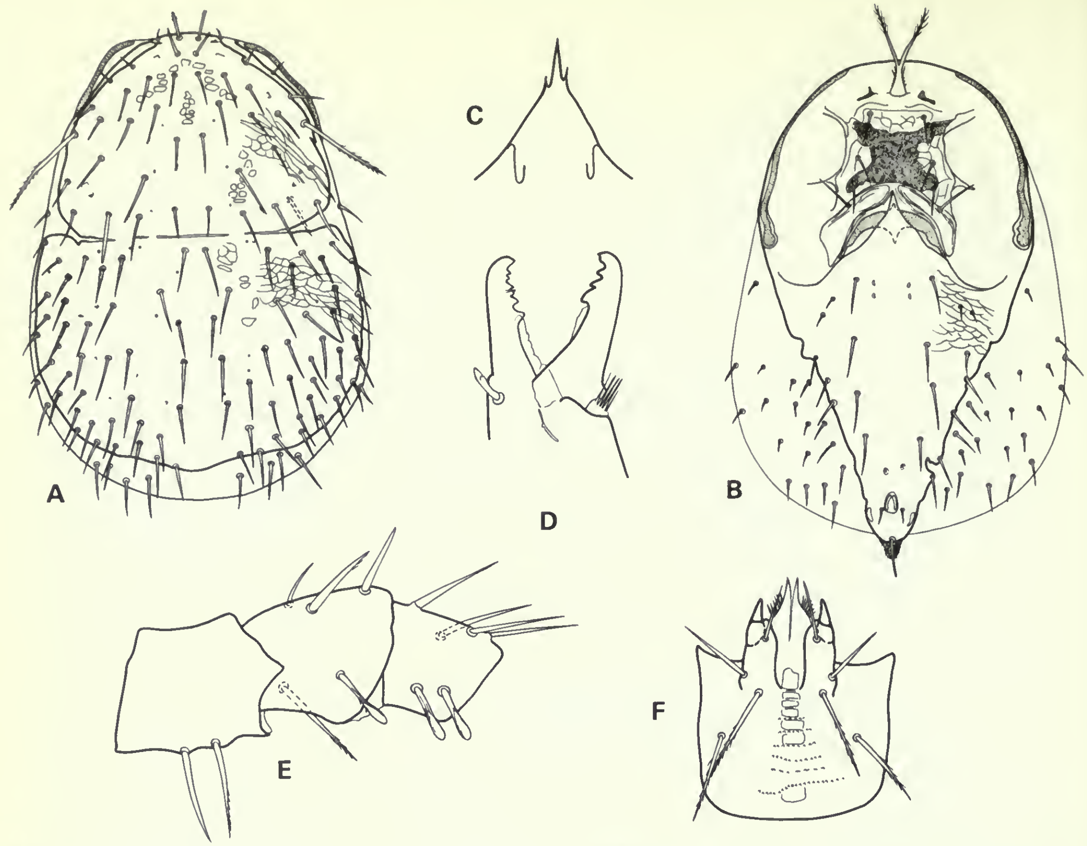

Fig. 59 *Poecilochirus austroasiaticus* Vitzthum, **female** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma.

MATERIAL EXAMINED. 5 samples – several hundred DNN, many ♂♂ and ♀♀.

ENGLAND: Two deutonymphs from a tripe and prepared-meat factory, Torquay, Devon, April 1958: many deutonymphs, males and females in maggots used for fish bait, Surrey, January 1964; many deutonymphs from a glue factory, Bermondsey, London S.E.16, probably around 1940–1945.

SCOTLAND: Five deutonymphs from silphid beetles – one from *Nicrophorus investigator* Zetterstedt and four from *Thanatophilus rugosus* (L.) – Balloch, Dunbartonshire, September 1978, Miss J. E. Christie coll.

DISTRIBUTION. This species is recorded for the first time from the British Isles.

It appears to have been found on the following occasions only: Vitzthum (1930*b*) based his original description on deutonymphs found on a camel corpse on the Siberia/Manchuria border in June 1927; Willmann (1939*a*, 1956) recorded deutonymphs from pitfall traps on high moorland in the Sudeten Mountains of Poland and Czechoslovakia; Holzmann (1969) recorded deutonymphs from meat bait near Erlangen, Germany; Karg (1971) recorded this species from pine litter and humus, presumably from Germany, and Davydova (1969, 1976) recorded it from Western Siberia.

Poecilochirus davydovae sp. nov.
(Figs 60A–F; 61A–K)

Poecilochirus subterraneus (Müller) sensu Davydova, 1969: 27, 28; 1976: 106.?Bregetova *et al.*, 1977: 99, 101.

Davydova (1969 and 1976) recorded *P. subterraneus* (Müller) from Western Siberia and

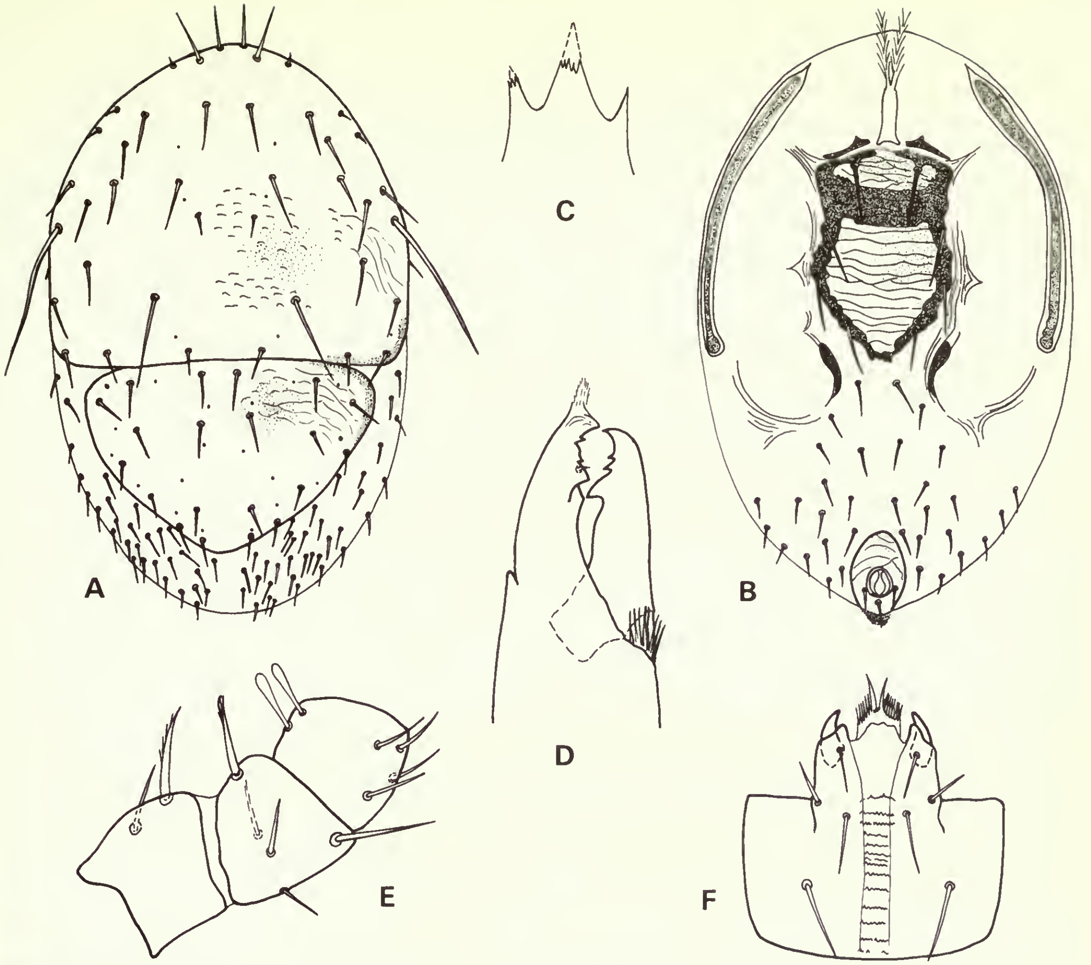

Fig. 60 *Poecilochirus davydovae* sp. n., **deutonymph** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma.

keyed and figured the deutonymph male and female. Although I have not been able to examine her specimens, her figures of the deutonymph are, I feel, clearly conspecific with specimens that I had considered to be of an undescribed species and are not *subterraneus* of Müller.

DEUTONYMPH. The podonotal shield measures 320–330 μm long × 360–380 μm wide (holotype 330 μm × 380 μm) and is well sclerotized, granular and completely ornamented with a pattern of broken reticulations (Fig. 60A). It bears 20 pairs of simple setae of which *z1*, *s1* and *s2* are minute (*c.* 8 μm) and *j5* are only slightly longer (10–12 μm). The longest setae are *r3* (*c.* 160 μm), which is also the stoutest, and *z5* (*c.* 100 μm). The remainder are up to *c.* 45 μm in length. The opisthonotal shield measures 190–200 μm long × 300–310 μm wide (holotype 200 μm × 310 μm), fits closely behind the podonotal, and is of similar texture. It bears ten pairs of simple setae in the specimen figured, but in some specimens one pair, *Z4*, are absent. All are *c.* 28 μm or less in length. The setae on the posterior membrane are slightly shorter, being around 20 μm.

The tritosternum has a narrow base and pilose laciniae. It is flanked by granular elongate presternal shields (Fig. 60B). The sternal shield measures from 200–220 μm in length (holotype 210 μm), is broad, transversely reticulated, and has a broad darkly sclerotized band between setae I and II which extends posteriorly as a continuous narrow border and curves

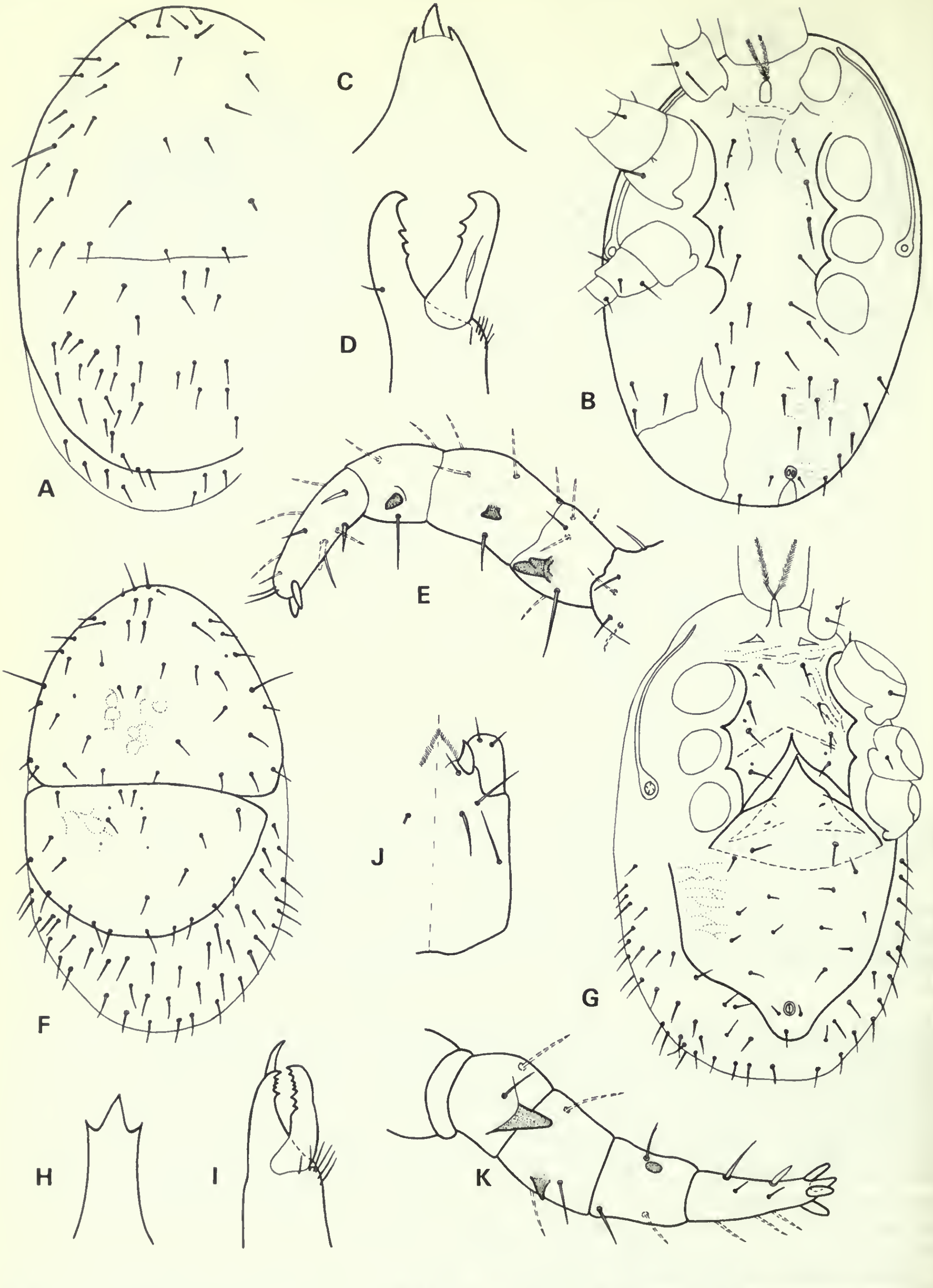

Fig. 61 *Poecilochirus davydovae* sp. n., **male** – A – dorsum; B venter; C tectum; D chelicera; E leg II: **female** – F dorsum; G venter; H tectum; I chelicera; J venter of gnathosoma; K leg II. All after Davydova, 1976.

anteriorly around setae I. The sternal setae are strong and slender. The endopodal shields may also be similarly heavily sclerotized, especially at coxae IV. The opisthogastric setae are simple and do not reach the bases of the next in line. The anal shield is elliptical, reticulated and finely granular, the three setae are simple. The peritreme extends to coxa I.

The tectum comprises a long flat process which distally is formed into a broad central prong flanked by a pair of shorter pointed prongs (Fig. 60C). The chelicera is shown in figure 60D. The membranous process at the tip of the fixed digit is sometimes short or weakly developed. The chaetotaxy of the palp trochanter, femur and genu (Fig. 60E) is similar to *P. subterraneus*. The venter of the gnathosoma is as in figure 60F: the corniculi are largely hidden by the hypostome. The leg setae are strong and simple and each leg bears a number of long erect dorsal setae, mainly on the femur, genu, tibia and tarsus as follows: leg I – femur 2, genu 1, tibia 1, tarsus 1; leg II – f. 3, g. 2, ti. 1, ta. 1; leg III – f. 1, g. 1, ti. 1, ta. 0; leg IV – f. 1 (the longest, *c.* 110 μm), g. 0, ti. 1, ta. 0.

MALE AND FEMALE. Figures 61A–E of the male and 61F–K of the female are based on Davydova (1976). The idiosoma of the male measures 640–678 μm long × 400–436 μm wide, and the female 778–850 μm long × 318–332 μm wide.

MATERIAL EXAMINED. 4 samples – 21 DNN.

ENGLAND: The first sample comprising the holotype (BMNH Reg. No. 1978. 11.9.1) and eight paratypes (1978.11.9.2–6); the second sample comprising four paratypes (1978.11.9.7–9), both from several specimens of *Nicrophorus vespilloides* Herbst (Silphidae), New Forest, Hampshire, 1971, coll. B. J. MacNulty; and two samples of paratypes from silphid beetles, Balloch, Dunbartonshire, September, 1978, coll. Miss J. E. Christie, which comprise six deutonymphs from *Nicrophorus vespilloides* and two deutonymphs from *Thanatophilus rugosus.*

Poecilochirus subterraneus (Müller)

(Fig. 62A–F)

Porrhostaspis subterranea Müller, 1860: 176.

Parasitus subterraneus: Oudemans, 1902*b*: 31.

Poecilochirus subterraneus: Berlese, 1904*b*: 280. Cooreman, 1943: 17. Bregetova, 1956: 62. Micherdzinski, 1969: 664. Holzmann, 1969: 7. Karg, 1971: 419. Non Davydova, 1969: 27, 28; 1976: 106 = *P. davydovae* p. 358.

DEUTONYMPH. The podonotal shield (336–360 μm long × 372–384 μm wide) tapers behind setae *r3* and is well sclerotized, granular and completely ornamented with a pattern of broken reticulations (Fig. 62A). It bears 20 pairs of setae of which *z1, s1* and *s2* are minute (*c.* 8 μm). The remaining setae are of varying lengths, stout, often sinuous, with *z5* (*c.* 142 μm) and *r3* (*c.* 200 μm) the longest. The opisthonotal shield (204–240 μm long × 276–312 μm wide) fits closely to the posterior taper of the podonotal and is similarly granular, but the reticulations are more elongate. It bears 11 pairs of stout setae which are shorter than those of the podonotal shield and of more even length. The posterior membrane bears shorter setae again.

The tritosternum has a narrow base and pilose laciniae. It is flanked by dark elongate presternal shields. The sternal shield (240–255 μm long) is broad, transversely reticulated and has a broad darkly sclerotized transverse band between setae I and II which extends posteriorly as a continuous narrow border and curves anteriorly around setae I (Fig. 62B). The sternal setae are strong and slender. The endopodal shields may also be similarly sclerotized, especially at coxae IV. The opisthogastric setae are strong, slender, and longest in the midventral region where they generally overlap the bases of the next in line. The anal shield is elliptical, reticulated, granular, and the three setae are simple. The peritreme extends to coxa I.

The tectum comprises a long broad process which is forked anteriorly into a central broad prong, which may itself be forked or simple, flanked by short lateral prongs (Fig. 62C). The

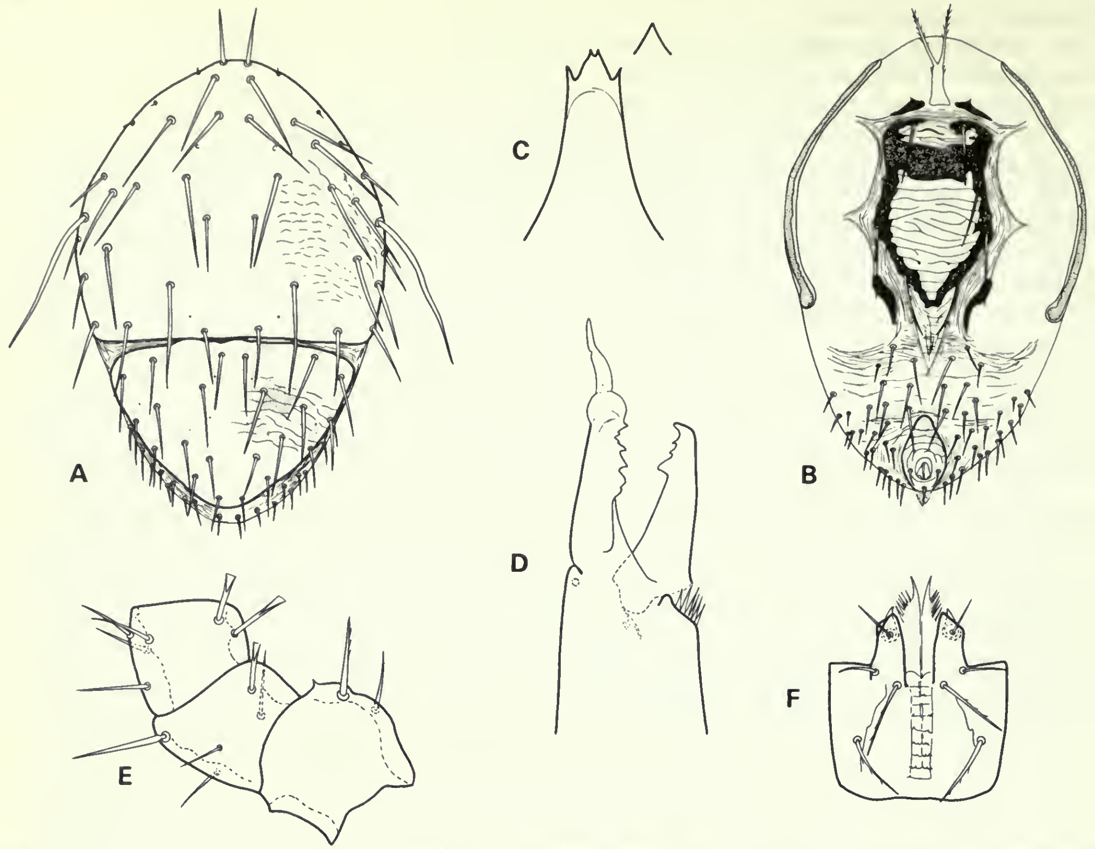

Fig. 62 *Poecilochirus subterraneus* (Müller), **deutonymph** – A dorsum; B venter; C tectum; D chelicera; E palp trochanter, femur and genu; F venter of gnathosoma.

chelicera is shown in figure 62D. The membranous process at the tip of the fixed digit may be broken off. The chaetotaxy of the palp trochanter, femur and genu is in figure 62E. The anterolateral setae on the femur and genu are alike, being spatulate distally and truncate. The distal dorsal seta on the femur is lancelike. The venter of the gnathosoma is shown in figure 62F. The corniculi are largely hidden by the hypostome. All leg setae are strong, appear simple, and each leg bears a number of long erect dorsal setae, mainly on the femur, genu, tibia and tarsus, as follows: leg I – femur 2, genu 1, tibia 1, tarsus 1; leg II – f. 3, g. 2, ti. 1, ta. 1; leg III – f. 1, g. 1, ti. 1, ta. 0; leg IV – f. 1 (the longest, *c.* 190 μm), g. 0, ti. 1, ta. 0.

MALE AND FEMALE. So far the adults of this species have not been found.
Holzmann (1969) has figured the larva.

MATERIAL EXAMINED. 45 samples – *c.* 240 DNN.
ENGLAND: Cornwall, Hampshire, Surrey, Buckinghamshire, Bedfordshire, Suffolk, Norfolk, Derbyshire, Cheshire, Lancashire, Yorkshire.
WALES: Pembrokeshire (Skokholm, Skomer).
SCOTLAND: West Lothian, Dunbartonshire.
IRELAND: No locality given, but from the same collection as some material noted under *Poecilochirus carabi* (p. 350)

The deutonymphs are found mainly on beetles of the widespread genus *Nicrophorus* (Silphidae). Of the forty-five samples examined only two were from other beetles, *Oiceoptoma thoracicum* (L.) (Silphidae) and *Aphodius rufipes* (L.) (Scarabaeidae), whilst one, a single deutonymph, was from leaf litter. Almost nothing is known of the development or biology of this species, although Holzmann (1969) figures the larva, and it is possible that occurrences on beetles of genera other than *Nicrophorus* are purely accidental (see also Cooreman, 1943).

DISTRIBUTION. This species has only been recorded from the British Isles by Springett (1968) from the Farne Islands, Northumberland, but it would appear from the material examined to be widely distributed.

It is recorded from Holland (Oudemans, 1902*b*, 1902*c*), Belgium (Cooreman, 1943), Germany (Oudemans, 1903*a*, Holzmann, 1969), Czechoslovakia (Müller, 1860), and the U.S.S.R. (Bregetova, 1956, Vysockaja & Bregetova, 1957). The record of this species from Western Siberia, given by Davydova (1969, 1976) is referable to *Poecilochirus davydovae* sp. nov. (p. 358).

Genus ***TRACHYGAMASUS*** Berlese

Trachygamasus Berlese, 1904. *Redia* **1:** 235; 1906. *Redia* **3:** 116.
Saprogamasus Willmann, 1949. *Veröff. Mus. nat.-Völker-Handelsk. Bremen* **A1:** 136.
Willmanniella Götz, 1969. *Acarologie* **13:** 24.

TYPE SPECIES. *Gamasus pusillus* Berlese, 1892*b*.

Dorsal shield of male entire, with transverse suture; female and deutonymph with separate podonotal and opisthonotal shields. Setae *z5* of dorsal hexagon differing in form from setae *j5* and *j6*. Tritosternum of male absent, of female and deutonymph normal, biramous. Metasternal shields of female either fused with the sternal shield or separated, in part or completely, by a transverse suture. Genital shield subtriangular. Opisthogastric shield of adults with normally not more than six pairs of setae. Setae *al* of palp femur and al_1 and al_2 of palp genu spatulate. Male chelicerae symmetrical. Corniculi short, entire. Legs of male, female and deutonymph without spurs. Pulvilli of legs II–IV with lateral lobes acuminate.

So far this genus is known only in the nymphal and adult stages. These are readily separated from the other parasitid genera by the presence of slender pointed lobes to the pulvilli of legs II–IV, whilst additionally, in the female, the junction between the sternal and metasternal shields is transverse (it may be very indistinct) and not oblique.

Nine species have been described, namely *Gamasus pusillus* Berlese, 1892*b* (DN, ♂, ♀), from Italy, *?Trachygamasus ohlini* Trägårdh, 1907 (?PN), from the Falkland Islands, *Saprogamasus ambulacralis* Willmann, 1949*b* (♂, ♀), from Germany, *Trachygamasus macfarlanei* Costa, 1962 (DN (not described), ♀), from Israel, *Saprogamasus gracilis* Karg, 1965 (PN, DN, ♂, ♀), from Germany, *Trachygamasus minor* Holzmann, 1969 (♂, ♀), from Germany, *Willmanniella fallax* Götz, 1969 (♀), also from Germany, *Trachygamasus medianus* Tichomirov, 1977, in Bregetova et al. (♀), from the southern U.S.S.R., and *Trachygamasus triangulus* Karg, 1978 (♀), from Chile.

Up till now there have been no records of *Trachygamasus* from the British Isles, but during the course of the present work six samples – five from Britain and one from Ireland – were examined which comprised 39 deutonymphs, one male and eleven females. All appear to belong to one species which by virtue of the measurements of the adults I am identifying as *ambulacralis* (Willmann). More recently, however, Professor G. O. Evans has sent me six deutonymphs and one female from two collecting sites in Ireland. These are all smaller than the specimens previously examined and were identified by Evans (*in litt.*) as *gracilis* (Karg), with which I agree. The adults only of *pusillus, ambulacralis* and *minor* are figured by Holzmann (1969) and *fallax* by Götz (1969), whilst Karg (1971) synonymizes *minor* with *gracilis.* Comparison of the British and Irish specimens with the published figures and descriptions have so far only established that two forms are represented and these are separable only on size: those which I am referring to *ambulacralis* are all larger than those referred to *gracilis.* The variations in setal lengths, form of the tectum and degree of sclerotization of dorsal and ventral shields are criteria that previous authors have emphasized as diagnostic features, but all variations occur within one sample. Professor M. Costa (pers. comm.) has pointed out that Karg's 1965 and 1971 papers contain contradictions, or at least changes of opinion, which tend to render more unstable the distinctions between species. Therefore, until more samples containing all post-embryonic developmental stages are collected I am not prepared to pronounce judgment on the validity of the known species or to be more commital on the identity of the few specimens so far recorded from the British Isles.

Trachygamasus ambulacralis (Willmann)
(Figs. 63A–I; 64A–I)

Saprogamasus ambulacralis Willmann, 1949*b*: 137. Micherdzinski, 1969: 612. Bregetova *et al.*, 1977: 97, 98.
Trachygamasus ambulacralis: Karg, 1971: 420.

DEUTONYMPH. The weakly sclerotized dorsal shields are finely reticulated (Fig. 63A). The podonotal shield (264–283 μm long × 264–316 μm wide) bears 20 pairs of setae, *s2* being generally situated off the shield. With the exception of setae *r3* and *z5*, which are stouter and longer than the remainder and are finely pilose distally, all setae are simple. The opisthonotal shield (162–210 μm long × 228–260 μm wide) bears 12–13 pairs of setae, the pair shown dotted in the figure being frequently situated on the membrane adjacent to the shield. Setae *S4* are stouter than the remainder and are finely pilose distally. The posterior interscutal membrane bears about 16 pairs of slender simple setae.

The tritosternum has a narrow base and pilose laciniae. It is flanked by a pair of triangular presternal shields (Fig. 63B). The sternal shield (*c.* 168 μm long), and the anal shield are very weakly sclerotized, the former is devoid of ornamentation and bears four pairs of fine simple setae, the latter bears the normal three setae all of which are simple. The stigma is situated adjacent to the posterior margin of coxa III and the finely granular peritreme extends anteriorly to the level of coxa I. The membrane posterior to the sternal shield bears approximately 12 pairs of fine slender simple setae. The metapodal plates are barely discernible.

The tectum most frequently has the centre prong broken off (Fig. 63C), but when entire it is similar to that of the female (Fig. 64E). The chelicera is shown in figure 63D. The chaetotaxy of the palp trochanter, femur and genu is as in the adults (Fig. 64G). The corniculi and gnathosomal setae are as in the female (Fig. 64H), whilst the hypognathal denticles are indistinct, about ten rows being present. Legs I–III bear fine simple setae, but leg IV, on which the setae are somewhat stouter, has in addition an erect pilose dorsal seta proximally which measures 85 μm in length. Pulvilli II–IV have the lateral lobes acute (Fig. 63E).

MALE. The dorsal shield (630 μm long × 340–361 μm wide) is entire but with a transverse median suture extending almost to the margins. It is reticulated except in the region between setae *z5* and *J5* which is almost devoid of ornamentation. The podonotal region bears 21 pairs of setae of which *j4, r3* and *z5* are stout and plumose distally as in the female (Fig. 64A). The opisthonotal region (Fig. 63F) bears from 32–38 pairs of setae of which *Z1* and *Z3* are stout and pilose distally, the remainder, in both regions, being slender and simple.

The tritosternum is absent. The genital lamina protrudes anteriorly from the holoventral shield and is flanked by a pair of squarish presternal shields (Fig. 63G). The five simple pairs of sternogenital setae are fine and slender, as are the six pairs of opisthogastric setae and the three anal setae. The stigma is situated opposite the posterior margin of coxa III and the finely granular peritreme extends to beyond coxa I.

The tectum is as in the female (Fig. 64E). The chelicera is shown in figure 63H. The chaetotaxy of the palp trochanter, femur and genu is as in the female (Fig. 64G). The corniculi are simple (Fig. 63I), but are, with the anterior hypostomatic setae, raised on stalk-like protuberances of the gnathosoma. The hypognathal denticles are not distinct, only six rows being readily discernible. All setae on the legs are simple and relatively slender. The males of *Trachygamasus* are unique in the Parasitidae in that there are no spurs or

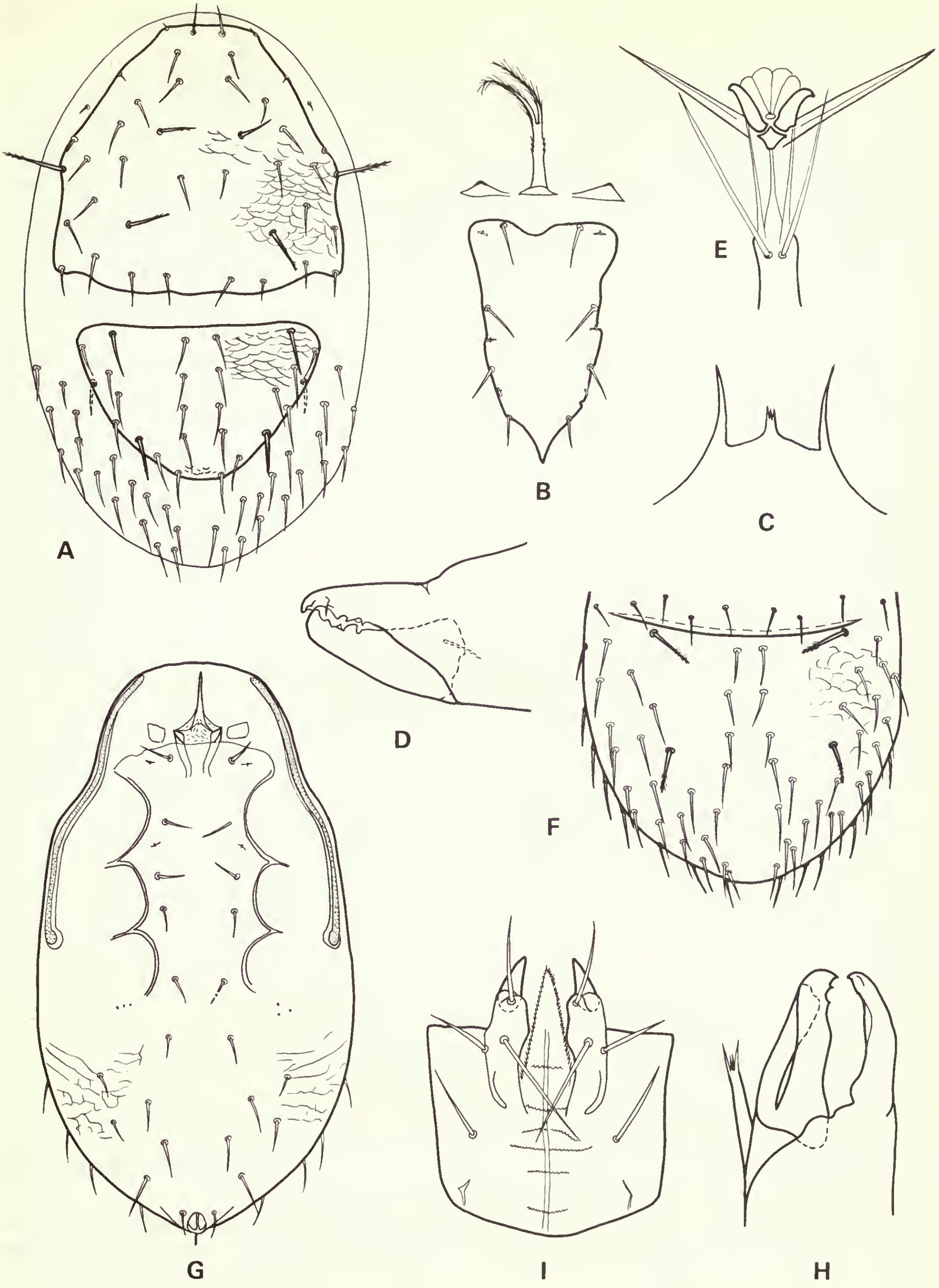

Fig. 63 *Trachygamasus ambulacralis* (Willmann), **deutonymph** – A dorsum; B sternal shield and tritosternum; C tectum; D chelicera; E pulvillus of legs II–IV: **male** – F opisthonotal region; G venter; H chelicera; I venter of gnathosoma.

hypertrophied setae on leg II. The pulvilli of legs II–IV have the lateral lobes acute as in the female (Fig. 64I).

FEMALE. The podonotal shield (350–430 μm long × 350–490 μm wide) is extensively reticulated and bears 21 pairs of setae of which *j4, r3* and *z5* are stout and pilose distally (Fig. 64A). The posterior margin is convex medially. The opisthonotal shield (300–470 μm long × 320–460 μm wide) bears a maximum of 18 and a minimum of 15 pairs of setae, several from the anterolateral margin being frequently situated on the adjacent membrane (Fig. 64B). Setae *Z1* and *Z3* are stout and pilose distally, the remainder being slender and simple. The laterally reticulate shield is concave anteromedially. The posterior interscutal membrane bears a dozen or more pairs of simple setae.

The tritosternum, which is typically bilaciniate, is flanked by small trapezoidal presternal shields (Fig. 64C). The granular sternal and metasternal shields, shown in detail in figure 64D, are separated by a transverse suture. Sternal setae I and IV are fine and slender, whilst II and III are shorter and stout. The genital shield is pointed anteriorly, but the lateral margins are irregularly formed. The genital setae are simple. The opisthogastric shield bears six pairs of simple setae and the anal setae are short and simple. One pair of setae on the membrane adjacent to the anus is pilose distally. The stigma is situated adjacent to the posterior margin of coxa III and the granular peritreme extends to beyond coxa I (Fig. 64B).

The tectum (Fig. 64E) is three-pronged with the central prong, which is frequently broken off, trifid end finelypectinate distally. The lateral prongs are also slightly pilose. The chelicerae (Fig. 64F), which are similar to those of the deutonymph, bear three symmetrical teeth on the movable digits, but less clearly defined teeth on the fixed digits. The palp trochanter, femur and genu are shown in figure 64G. The corniculi are plain (Fig. 64H), the gnathosomal setae simple, and from ten to twelve rows of hypognathal denticles are discernible. All setae on the legs are simple. The ambulacra of legs II–IV have the lateral lobes of the pulvilli acute (Fig. 64I).

MATERIAL EXAMINED. 6 samples – 40 DNN, 4 ♂♂, 12 ♀♀.

ENGLAND: From sewage filter-beds, Birmingham, 1966, 1975; from mosses, rushes and damp grasses, Startops End Reservoir, Buckinghamshire/Hertfordshire borders, 1 February 1964; moss and humus, Bath, Kennet and Avon Canal, Somerset, 10 March 1962.

SCOTLAND: From nest of water vole *Arvicola terrestris* (L.), near Aberdeen, 3 December 1965.

IRELAND: From seaweed, Bell Harbour, Co. Clare, September – October 1961.

DISTRIBUTION. Previously known only from Germany (Willmann, 1949*b*, Holzmann, 1969, Karg, 1971) where it has been scantily recorded on agricultural land from rotting vegetables, especially root crops, and from damp meadows and woodland.

Trachygamasus gracilis (Karg)

Saprogamasus gracilis Karg, 1965: 300. Bregetova *et al.*, 1977: 98.
Trachygamasus gracilis: Karg, 1971: 420.
Trachygamasus minor Holzmann, 1969: 23. Karg, 1971: 420.

As stated above, I can see no constant differences, apart from size, between the species identified here as *Trachygamasus ambulacralis* (Willmann) and *T. gracilis* (Karg). The following are the main measurements of the *gracilis* specimens:

DEUTONYMPH. Podonotal shield 212–240 μm long × 200–235 μm wide, opisthonotal shield 125–150 μm long × 167–202 μm wide, sternal shield 137–155 μm long. The erect dorsal seta on tarsus IV is 57–60 μm long.

MALE. Not collected.

FEMALE. Podonotal shield 250 μm long × 262 μm wide, opisthonotal shield 225 μm long × 250 μm wide.

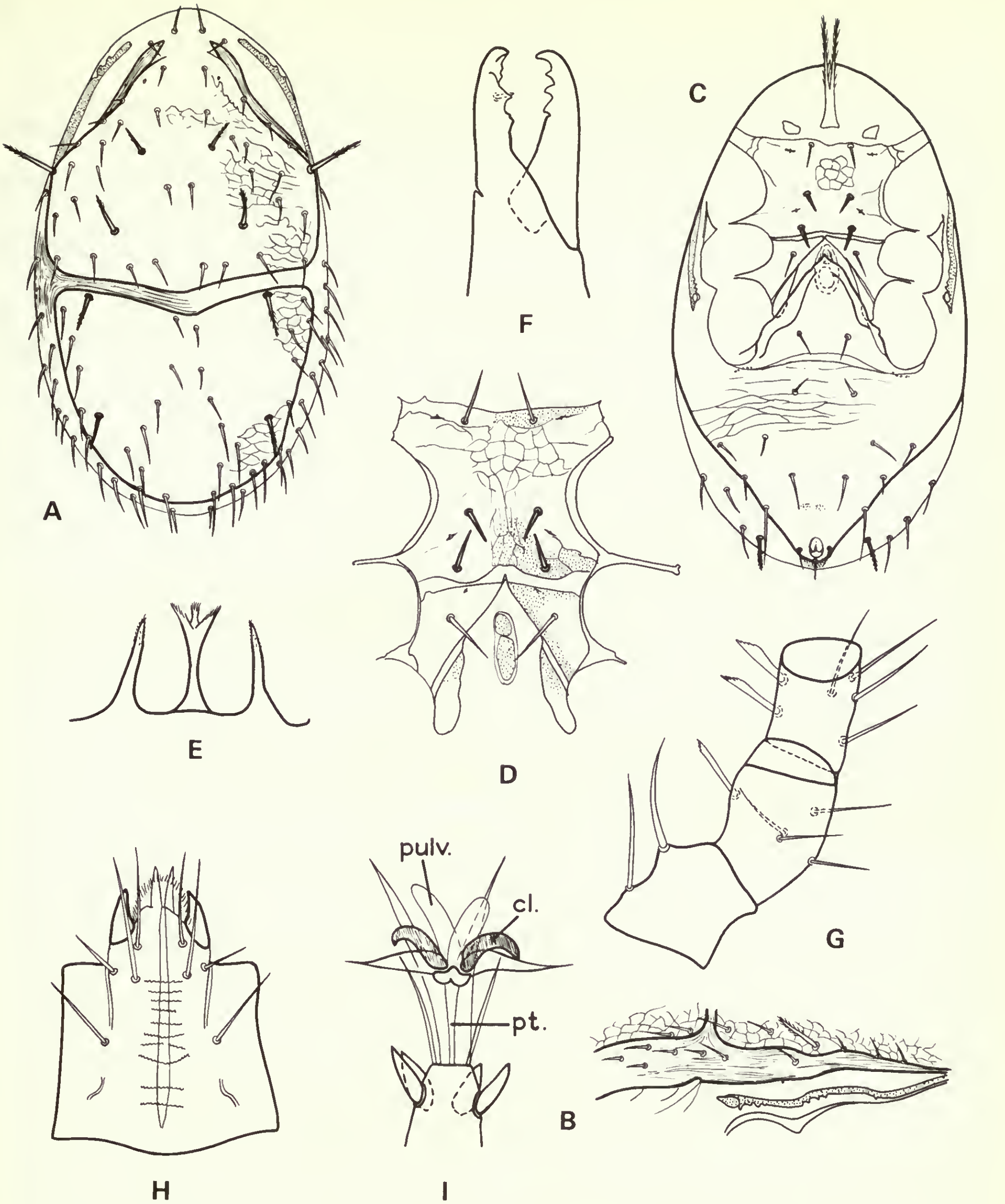

Fig. 64 *Trachygamasus ambulacralis* (Willmann), **female** – A dorsum; B lateral interscutal region; C venter; D sternogenital region; E tectum; F chelicera; G palp trochanter, femur and genu; H venter of gnathosoma; I ambulacrum of legs II–IV. Abbreviations in text, p. 246.

MATERIAL EXAMINED. 2 samples – 6 DNN, 1♀.
IRELAND: Meath; Grange, and Kildare; Celbridge, both in grassland.

DISTRIBUTION. Previously known only from Germany (Karg, 1965, 1971 and Holzmann, 1969) where it is scantily recorded from cucumber soil in greenhouses and from cowdung.

Taxonomic summary

(*a*) *Poecilochirus davydovae* sp. nov. is described.

(*b*) The following new synonymy is presented:

Eugamasus spinosustarsis Schweizer, 1961, is a synonym of *Eugamasus magnus* (Kramer, 1876).

Parasitus eta Oudemans & Voigts, 1904, is a synonym of *Parasitus fimetorum* (Berlese, 1904).

Parasitus anglicus, bombophilus and *numismaticus*, all Vitzthum, 1930, are synonyms of *Parasitellus talparum* (Oudemans, 1913).

Parasitus crinitosimilis and *dubiosus,* both Vitzthum, 1930, are synonyms of *Parasitellus crinitus* (Oudemans, 1903).

Parasitus hibernicus Turk & Turk, 1952, is a synonym of *Parasitus fimetorum* (Berlese, 1904).

Parasitus lunarisimilis Schweizer, 1961, is a synonym of *Gamasodes spiniger* (Trägårdh, 1910).

Poecilochirus necrophori Vitzthum, 1930, is a synonym of *Poecilochirus carabi* (G. & R. Canestrini, 1882).

Poecilochirus nordi Davydova, 1969, is a synonym of *Poecilochirus austroasiaticus* Vitzthum, 1930.

(*c*) The following new combinations are proposed.

Parasitellus crinitus (Oudemans, 1903)
Parasitellus ignotus (Vitzthum, 1913)
Parasitellus talparum (Oudemans, 1913)
Vulgarogamasus kraepelini (Berlese, 1905)
Vulgarogamasus oudemansi (Berlese, 1904)

Species new to the British Isles

Eugamasus cavernicola Trägårdh, 1912
Eugamasus magnus (Kramer, 1876)
Gamasodes fimbriatus Karg, 1971
Parasitellus crinitus (Oudemans, 1903)
Parasitellus ignotus (Vitzthum, 1930)
Parasitus beta Oudemans & Voigts, 1904
Parasitus copridis Costa, 1963
Parasitus evertsi Oudemans, 1902
Parasitus hyalinus (Willmann, 1949)
Parasitus insignis (Holzmann, 1969)
Poecilochirus austroasiaticus Vitzthum, 1930
Poecilochirus davydovae sp. nov.
Trachygamasus ambulacralis (Willmann, 1949)
Trachygamasus gracilis (Karg, 1971)

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